Functional morphology and productivity of a tussock grassland in the Bolivian Altiplano

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José Alberto Fernandez Monteiro
aus Santos, SP, Brasilien

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Prof. Dr. Christian Körner
PD Dr. Andreas Lüscher

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Prof. Dr. Eberhard Parlow
Dekan

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1.0 General Introduction

Tall tussocks dominate large areas of tropical and subtropical highlands (Cuatrecasas, 1968; Hedberg, 1964; Löffler, 1979; Ramsay and Oxley, 1997; Hnatiuk, 1994) and extend into cool maritime climates of the southern hemisphere temperate zone (Mark et al., 2000; Oliva et al., 2005). Their dominance seems to be associated with year round cold climate, but otherwise quite different soil moisture regimes from very wet (New Guinea, New Zealand, Ecuador) to rather dry, even semi-arid, as is the case in the NW-Argentinean and the Bolivian Altiplano (Geyger, 1985; Halloy, 1982). The compact morphology contributes to the accumulation of dead material, which forms a large intra-tussock litter component. In undisturbed areas, the amount of litter can exceed above-ground phytomass 2.5-fold, and above-ground biomass 10-fold (Hofstede et al., 1995*b*).

Primary production in tropical mountains is still unknown. The classic and simple method of harvesting after the peak of the growing season does not work for perennial year-round active vegetation, since it is impossible to distinguish the phytomass produced during the observation from the phytomass present a priori. In the temperate alpine zone, grasslands produce 200–300 g m^{-2} of biomass per total land area in a 2–3 month growing season (Körner, 2003), accordingly, under no water restriction, one would expect 1200 g m^{-2} of biomass produced over a 12 months tropical season. The first non-destructive attempt to estimate high elevation tussock gross productivity was undertaken by Williams (1977), in New-Zealand, based on the length of new leaves produced per tiller per time, the weight to length ratio of leaves, and the tiller density per total land area, yielding 330 g m^{-2} for *Chionochloa macra* and 518 g m^{-2} for *Chionochloa rigida* per total land area, for a growing season of 7.5 months in areas with an average tussock land cover of 20%. A second assessment with this method resulted in 550 g m^{-2} (over 256 days) for *C. ririda*, 628–834 g m^{-2} (two sites over 148–228 days) for *C. macra*, and 843 g m^{-2} per land area (over 219 days) in a region of co-dominance of both species (Meurk, 1978), and land cover ranging from 23–83%. Similar attempt for the tropics suffered from non-regular census, short observation periods, and a number of simplifications that altogether cast doubt at the validity of the data obtained. Hnatiuk (1978) estimated a biomass production of 128–442 g m^{-2} per total land area (range of means for 6 sites) for *Dechampsia klossii* tussocks at 3200–4380 m a.s.l. on Mt Wilhelm, New Guinea, in a year-round wet growing season. Using the same method, Hofstede et al. (1995*a*) arrived at 198 ± 74 g m^{-2} for undisturbed and 308 ± 175 g m^{-2} for moderately grazed conditions (mean ± se, year-round growing season) in the Colombian Páramos. However, without accounting for rates of leafing and tillering, the method assumes a constant number of

growing leaves, so that a recently emerging leaf would immediately substitute a leaf that reached full length. Ramsay and Oxley (2001) reported 168–295 g m^{-2} based on harvesting data for unfertilized areas of the Ecuadorian Páramos. They used the phytomass in areas outside the studied plots to evaluate the initial phytomass per total land area, and than compared it with the phytomass of the fenced, studied areas after 103–110 days. Unfortunately, they did not separate biomass from necromass. Taken together, all these examples suggest a high elevation (alpine) grassland biomass production per year in the tropics anywhere between 100 and 800 g m^{-2} a^{-1}, perhaps 150–450 g m^{-2} a^{-1}.

Festuca orthophylla dominates vast areas in the Andean Altiplano, spreading from north-west Argentina, to Central Peru, from the Chilean Andes to the east edge of the Altiplano, between 3600 and 4680 m a.s.l., largely around 4000 m (as evidenced by archive data of various herbaria). In the dry pajonales, *F. orthophylla* is often the single species, but eventually shares space with woody shrubs of the genera *Bacharis* and *Parastrephia*. Small annual and perennial herbs may be found in the inter-tussock space during the rainy summer only, and despite their high nitrogen content, their contribution to annual biomass production is very small (Patty et al., 2010). *F. orthophylla* is the dominant component of the primary production in this system and of the diet of wild and domesticated camelids. The reason for the absence of tree species in the whole Altiplano, far below the tree line ecotone (Hoch and Körner, 2005), is not yet resolved (Ellenberg, 1996; Hammen and Cleef, 1986; Wesche et al., 2008). Pollen records from the sediments of Lake Titicaca (3812 m a.s.l.) indicate an increase in Poaceae abundance *ca.* 17700 BP. Since this increase in abundance of graminoids preceded the raise of charcoal (13200 BP), fire does not seem to be the only cause of this shift (Paduano et al., 2003). Yet, recurrent fire selects for plants with below-ground meristems and rapid re-growth potential after fire, and may be the cause of a shift from woodland to tussock grassland (Spehn et al., 2006). In addition to fire, grazing and trampling tolerance drive selection in favour of the large tussocks, leading to vast almost monospecific land cover.

To determine the annual biomass production of this montane, tropical grassland, an experimental site was established in the Sajama National Park, Bolivia (S 18° 08' W 68° 58' at 4250 m a.s.l.) on March 2006. The first step was to study in detail the morphology and dry matter allocation of *Festuca orthophylla*. In a second step, a non-destructive growth analysis was employed, using ramet demography and land cover data. Four 25 × 25 m parcels were fenced to exclude wild and domesticated grazers and to study the growth of *Festuca* tussocks in undisturbed condition. In addition, four areas were marked and left unfenced as control, to evaluate the impact of grazing on production. Additionally, the effect of dry llama dung addition, and clipping (down to 10–15 cm from the soil) or burning of tussocks on tussock growth was studied, to assess the consequences of tussock management and explore options of ameliorating pasture quality.

This doctoral thesis

Within the framework of my dissertation, I addressed three core questions of Altiplano tussock ecology; (1) the functional morphology of tussocks, (2) tussock land cover and

tussock productivity and (3) tussock leaf dynamics and potential compensatory responses to defoliation.

Chapter 2 explores the climatic life conditions and the functional morphology of the tussocks, the modular structures such as leaf, tiller, ramet, and the position of the meristems. This chapter also explores phytomass partitioning and biomass allocation, and the consequences for light interception also with regard to the high amount of intra-tussock dead plant material.

Chapter 3 presents a non-destructive assessment of biomass production, based on new leaves produced per ramet in each season, ramet density per tussock area and tussock land cover. These data were collected in fenced and non-fenced (grazed) areas. In addition, growth responses to camelid dung, clipping or burning were studied in both fenced and non-fenced areas. Together with the ramet censuses, ramet mortality and flowering were studied across seasons. Root in-growth cores were used as a proxy to test treatment responses of roots. Using aerial photographs and the line intercept method tussock cover was quantified in order to scale tussock based data to landscape scale.

Chapter 4 explores leaf dynamics, leaf duration and the question of compensatory growth after defoliation. It was hypothesized that under a low to moderate clipping (grazing) pressure, remaining leaves of clipped tillers would compensate for defoliation by enhanced growth. This part of the thesis involved measurements of initial leaf growth rate, final leaf length, onset of leaf senescence, leaf longevity and the frequency of leaf emergence for both tillers in the centre and the periphery of *Festuca orthophylla* tussocks. These data were collected for the rainy and the dry season.

2.0 Functional morphology and microclimate of *Festuca orthophylla*, the dominant tall tussock grass in the Andean Altiplano

2.1 Abstract

Plant growth is driven by the rate of photosynthetic uptake of carbon, the loss of carbon and by allocation of photoassimilates to certain plant compartments, which leads to particular morphologies. Performance, vitality and persistence of a plant are affected by this partitioning process and vice versa. Under harsh climatic conditions such as cold temperature and seasonal drought, perennial plants often invest more in below-ground than above-ground structures. *Festuca orthophylla* in the subtropical Bolivian Altiplano does not match this 'rule'. This species produces tall, evergreen tussocks, persisting decades and dominating the semi-arid, andean landscape over thousands of square kilometres at elevation between 3600 and 4600 m a.s.l. The shallow rooting system represents only 21% of total biomass. The tussock base (root-stocks composed of the network of branching below-ground shoots and tiller meristems), comprises 28% of the total biomass. Although partly below the soil surface, much of this biomass compartment is functionally above-ground (the basis of shoots). With their below-ground position, tiller meristems are protected against grazing and trampling by camelids as well as, to some degree, against fire and freezing. Fifty one percent of the biomass is above-ground (live leaves and inflorescences). In terms of phytomass (including attached necromass), 75% is above-ground. On average, a tussock consists of 3200 tightly packed total tillers (56% are live). Tillers emerge regularly intravaginally (*i.e.* within the leaf sheath of an existing mother tiller), resulting in dense canopies with strong self-shading: eighty percent of green foliage experience less than 50% of the incident light. The most important Altiplano plant species thus, exerts morphological traits in favour of protection and survival rather than productivity.

2.2 Introduction

Tall tussocks dominate large areas of tropical and subtropical highlands (Cuatrecasas, 1968; Hedberg, 1964; Hnatiuk, 1994; Löffler, 1979; Ramsay and Oxley, 1997) and extend into cool maritime climates of the southern hemisphere temperate zone (Mark et al., 2000; Oliva et al., 2005). Their dominance seems to be associated with year round cold climate but otherwise quite different soil moisture regimes from very wet (New Guinea, New

Zealand, Ecuador) to rather dry, even semi-arid, as is the case in the NW-Argentinean and the Bolivian Altiplano (Geyger, 1985; Halloy, 1982).

With their massive root-stock, compact clonal growth and great longevity, these tussocks play a key role in erosion control and thus, can be considered as 'landscape engineers'. This role becomes essential for soil conservation, when overgrazing leads to an almost complete loss of the wet-season-active inter-tussock vegetation, as is the case in our test region. Nevertheless, recent increases in grazing pressure and a shift in livestock type (different animals) may lead to a weakening, and eventually, a collapse of the tussock vegetation. Large areas of bare soil where vegetation was burnt as part of the traditional land management do not seem to recover from fire (observation by J. Monteiro). Grazing camelids, llamas in particular, feed on leaves and inflorescences, and heavily trample the inter-tussock space, thus reducing the reproductive potential of *Festuca orthophylla* and as a consequence, young tussocks are very rare. Furthermore, as the camelids prefer fresh, regrown leaves, resprouting after burning is limited when tussocks are not protected from grazing.

Festuca orthophylla is the most widespread and characteristic grass species of the tropical and subtropical andean (*sensu* 'alpine') Altiplano, covering large areas in Bolivia, Chile, Peru and Argentina, between 3600 and 4680 m a.s.l., largely around 4000 m (as evidenced by archive data of various herbaria, compiled by J. Monteiro). The tussock height of *Festuca orthophylla* varies from *ca.* 0.40 m in NW Argentina to nearly 1.5 m in slightly more favourable areas in Bolivia (mostly around 0.6 m in height). Though tussocks are initially confined to a compact circular shape, they form rings with a bare centre as they get older. These circles often become fragmented and may end up as linear clonal structures. In NW-Argentina, they form garlands which progress in a wave-like manner through the high plateaus (Halloy, 1982; Körner, 2003), whereas in Bolivia, at similar elevation, the compact, circular forms and fragments of collapsed rings dominate.

Past vegetation reconstructed from pollen records from the sediments of Lake Titicaca (3812 m a.s.l.) indicates an increase in Poaceae abundance *ca.* 17700 BP. Since this increase in abundance of graminoids preceded the raise of charcoal (13200 BP), fire does not seem to be the only cause of this shift (Paduano et al., 2003). Yet, recurrent fires do select for life forms with protected below-ground meristems and high resprouting potential. Fire eliminates competing shrubs and may lead to almost monospecific stands of tussock grassland as is the case with *Festuca orthophylla* in the study area, at 4250 m altitude in Bolivia. In addition to fire, grazing and trampling tolerance represent a second set of selective drivers in favour of tall tussocks. However, grazing alone is not considered a destructive disturbance for these tussocks, after having survived centuries of land use (Preston et al., 2003).

Due to their spatial dominance these tussocks also form the single largest component of biomass and productivity over large upland areas. However, the productivity of these areas is unknown, because productivity cannot be assessed with the classical harvesting methods, given the continuous production of new plant tissue and the great longevity of tillers. This is a general problem for tropical and subtropical grassland, high elevation ones in particular (Körner, 2003), and the problem has not yet been solved. Hnatiuk (1978) was the first to explore tropical-alpine tussock productivity with the only possible,

non-destructive method, a tiller turn-over study, but given the long observation periods required and the miserable working conditions on Mt. Wilhelm in New Guinea, this did not lead to useful data. It is quite obvious, that such an analysis requires a very good understanding of the morphology and growth strategy of such tussocks, one of the tasks of this study. Ultimately, it is tiller and leaf demography, longevity and turnover rates that will convert into estimates of productivity. Such census work depends on the use of comparable morphological units. In the case of *Festuca orthophylla*, it is not obvious at first sight, what is a leaf, what a tiller and what a ramet unit. The situation becomes further complicated by the fact that ongoing grazing by camelids (llama, alpaca, vicuña) interferes with any census work. Clipping and observing immediate re-growth would lead to a substantial overestimation of sustainable productivity, because of the potential compensatory growth response to such disturbance (Belsky et al., 1993; Ferraro and Oesterheld, 2002; Loeser et al., 2004; McNaughton, 1983*a*). Regrowth after disturbance depends on a massive root-stock and root system ('stored growth'); the size of which and the interconnectedness of tillers may hold part of the explanation for the success of this species under the combined influence of a stressful environment and intense grazing. Before productivity can be assessed with a demographic approach, the morphology and biomass allocation needs to be understood. Specifically, we are asking the following questions: (1) What is the intra-tussock clonal structure, the architecture of ramification and tillering, and how are individual tillers and roots 'constructed'? (2) How is biomass partitioned among the various live compartments of a given tussock, and what is the fraction of live *versus* standing-dead phytomass? And (3) we ask how these structures are arranged, and thus, are influencing the internal light and temperature regime in the tussock? We are presenting a combination of a morphological analysis and an assessment of the biomass allocation that will serve as a reference for productivity studies in tall tussocks in subtropical and tropical grasslands. In follow-up papers we will present productivity studies under the influence of camelid exclosure (fences), burning, clipping and llama dung application (Chapter 3).

2.3 Material and methods

2.3.1 Study site

The study site was located in the Sajama National Park in western Bolivia, close to the border to Chile (S 18° 08' W 68° 58' at 4250 m a.s.l.). Over large areas, the tall tussock-forming grass *Festuca orthophylla* is the dominant species occasionally associated with shrubs of the genera *Baccharis* and *Parastrephia* ('thola'). Herbaceous species play a minor role and appear during the wet season only (Patty et al., 2010).

Rainfall is very low (annual amounts of 300–350 mm, cf. Hardy et al., 1998) and is restricted to November to March (austral summer). The warmest period of the year coincides with highest rainfall. Monthly means in air temperature range from 2.3° C (coolest month, July) to 10.7° C (warmest month, December). However, temperature data revealed pronounced temperature variation per day, from freezing to temperature of more than 30° C.

2.3.2 Weather data, tussock light and temperature regime, soil moisture

Air temperature was measured hourly from August 2003 till August 2008 with temperature loggers (TidbiT, Onset, USA), at 2.80 m height above soil surface in complete shade. A rain gauge (RainWise, USA) was mounted on a roof in the village Sajama in May 2006 and running till August 2008.

Two temperature loggers (the same as for air temperature) were installed directly at the raised centre of two tussocks, close to the shoot meristem zone, 5–8 cm above surrounding terrain and screened by litter and necromass (Fig. 2.1), three loggers were buried −10 cm under bare ground (two under untreated inter-tussock space, one under llama dung, a treatment belonging to our productivity studies that will only be referred to for its potential effect on soil temperature and soil moisture). Tussock and soil loggers were exposed for almost 2 years (April 2006 to March 2008), the single logger under llama dung for one year (March 2007 to March 2008). Additional loggers were installed inside undisturbed *Festuca* tussock canopies, at 35 cm and 45 cm above the surrounding soil, fully shaded by aluminium screens (running for 16 days only: 18 February to 5 March 2008, taking temperature readings every 10 minutes).

For assessing the internal light regime of the canopy, we selected 3 *Festuca* tussocks (mean diameter of 0.50 m, mean height of 0.70 m) and we measured the light inside the tussock canopy following a horizontal and vertical grid (5 cm distance between each grid/measuring point) using a photon flux sensor (LI-189, LI-COR, USA) fixed on a 0.75 m long aluminium rod. After each light measurement inside the tussock, light conditions outside the tussock were measured. Inside tussock light readings were then expressed as a percentage of the ambient photon flux. We classified these relative light transmissions into 5 zones: (1) 75% to 100% transmission, (2) <75% to 50%, (3) <50% to 25%, (4) <25 to 10%, and (5) less than 10% light transmission. Phytomass was than clipped and sorted in relation to the different light zones and further separated into live, senescent, and dead parts. Because of the large size of tussocks, the phytomass harvest was restricted to one representative quarter sector of the whole tussock.

Volumetric soil moisture was measured adjacent to *Festuca* tussocks (n = 8; under the leaf canopy) and in the inter-tussock space (bare soil, n = 8), half of these measurements was taken in areas covered by llama dung. Sensors were installed at a soil depth of *ca.* 8–10 cm in April 2007 (sensor with a 45° angle to soil surface, flat side of the sensor in a vertical position; EC-10 probes, Decagon Inc., USA, Fig. 2.1). Volumetric soil moisture readings were taken sporadically by a hand-held meter (ECH2O CHECK, Decagon Inc., USA) connected to the probes, starting at the end of the rainy season 2006/2007 and over the complete rainy season 2007/2008 (total of 62 daily records over a 12 month period).

2.3.3 The tussock life form

We defined the height of a tussock as the mean distance between the ground surface near the tussock periphery and the majority of the tips of the central tillers, neglecting single, protruding leaves and inflorescences. Tussock diameter was measured as the outer periphery of the leaf canopy. The means presented are derived from maximum diameter

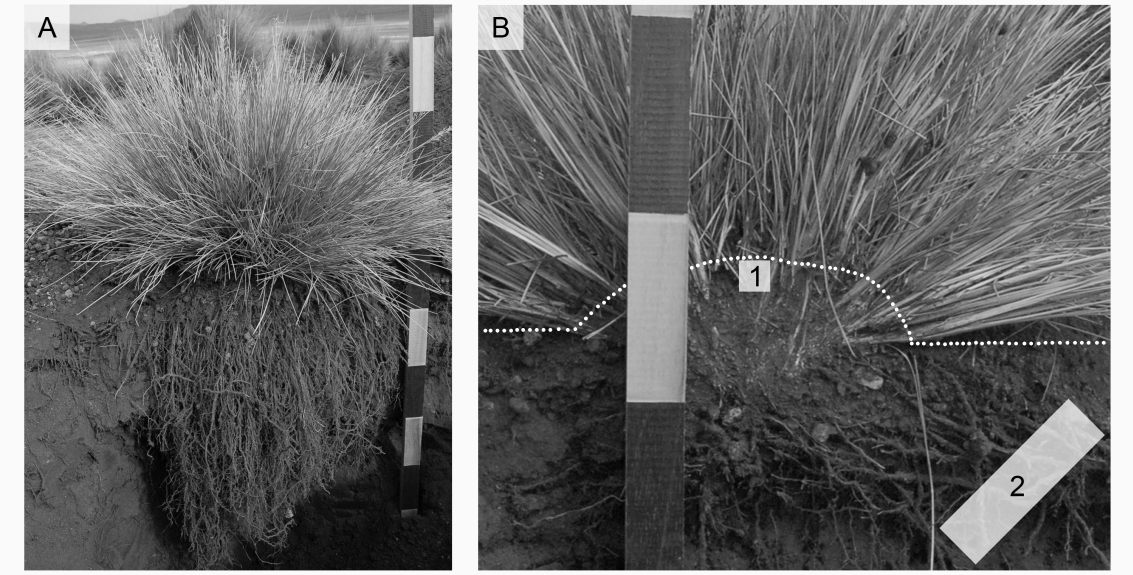

Figure 2.1: *Festuca orthophylla* in the Bolivian Altiplano (4250 m a.s.l.). (A) Medium size tussock with excavated root system (reference scale with 10 cm units). Notice: roots are not in natural position, but hanging down. Very few roots grow below 50 cm soil depth. (B) The transverse section illustrates the transition from the compact root-stock to above-ground structures. The dotted line shows the elevated tussock base; meristems are below this line. Number 1 indicates the position of the temperature logger, number 2 indicates the position of the soil moisture probe below the tussock canopy (for colour figure see electronic version

(d1) and the diameter at right angle to the maximum diameter (d2). The tussock area was calculated using the equation for an ellipse [$A = \pi \times (d1/2) \times (d2/2)$]. Height and mean diameter were measured in 160 tussocks and fragments of disintegrated tussocks in an area of 132 m^2.

2.3.4 Clonal structures and tiller morphology

To understand the architecture of individual tillers and their clonal connectivity, we had to isolate ramets including the bases of tillers, without breaking them apart, carefully wash off the sandy substrate and remove all attached dead material. To identify the position of apical meristems of tillers, we prepared longitudinal sections through the tiller base. Metabolically active zones (meristems) were stained with 2,3,5-triphenyltetrazolium chloride (TTC; Sturite et al., 2005). TTC is reduced into the red formazan by several plant enzymes (reductases, dehydrogenases), therefore staining by formazan occurs only in living plant cells, and the intensity of staining is an indicator for metabolic activity. Root-stock fragments (containing bases of 3-5 tillers) were incubated in 50 ml 0.06 M phosphate buffer in air tight, 250 ml beakers. After adding 50 ml 0.6% (w/v) TTC, the beakers were immediately vacuated with a hand vacuum pump to reduce the oxygen partial pressure, and then incubated at 30° C for 1 hour. Afterwards, non-reduced TTC was rinsed off with phosphate buffer, and samples were studied under a dissecting microscope (M5A 6–50×, Wild AG, Switzerland) and digital images were taken using macro-lens.

2.3.5 Tussock phytomass allocation and intra-tussock litter

We randomly selected tall but still compact, circularly shaped tussocks (no decaying centre), thus, very young and very old age classes were excluded. To assess the total tussock phytomass and its partitioning into above-ground biomass (live), attached necromass and intra-tussock litter, we sampled 9 bulk tussocks, 3 in the particularly dry year of 2007 and 6 in the rather normal year of 2008 (Tab. 2.1). It is near to impossible to arrive at the classical distinction of dead attached (*i.e.* necromass) *versus* dead detached (*i.e.* litter) material, because any standing dead material could still be attached to live structures below the soil surface. We pooled standing necromass forming tillers and dead leaves still attached to live tillers and considered this material as necromass; dead material that detached during harvesting was combined with intra-tussock litter. Given the bulk of dead material is standing, because it is protected from wind and animals by surrounding active tillers, necromass may include a substantial fraction of material that would represent litter in other vegetation types.

We assumed that the basic phytomass allocation patterns are equal in any given sector of the round tussocks, permitting us to harvest sectors only, in few cases one quarter, but mostly one eighth. The sectors for above-ground phytomass and intra-tussock litter were first cut vertically with a long knife and a spade down to 0.1 m below ground. Once the sector was isolated, we separated all tillers from the root-stock (dotted line in Fig. 2.1), categorized tillers into length classes by 10 cm steps, and sorted the harvested material into attached dead and live, as well as intra-tussock litter. The root-stock compartment

contained the basal (below-ground) part of tillers, the basal meristematic zone of each tiller, and the network of branching below-ground shoots, all together forming a compact body, infiltrated with sandy soil and decaying litter. This 'root-stock' is below the soil surface, but part of it (tiller basis) is functionally above-ground (Körner, 2004).

After sorting, the material was air dried in a solar tent (used in the Altiplano to desiccate llama meat) for at least 20 days. During this period, sub-samples were taken from the tent and oven-dried at 60° C for one hour. By comparing the dry weights, it was concluded that samples were fully dry after 3 weeks exposure in the solar tent.

For the three tussocks in which one quarter was harvested, we also excavated the roots as deep as 1 m. Roots and root-stocks were separated, root-stocks were cleaned and roots were carefully washed and sorted for diameter larger or smaller than 1 mm (fine roots). It was not possible to sort below-ground material into live and dead fractions, all roots and the root-stock attached to the plant was assumed to be live (clearly an overestimation in the case of root-stock, given the inclusion of dead leaf sheaths and basal parts of dead flowering stalks). The root material was dried in the solar tent for one week, and then re-dried in a common oven for one hour at 60° C and weighed.

2.3.6 Statistical analysis

Temperatures readings taken at 10 min intervals were averaged to hourly means. Daily minimum, mean and maximum temperatures within *Festuca* tussocks were compared to daily minimum, mean and maximum air temperatures during coolest and warmest months of the years 2006–2008. Corresponding comparisons were carried out to test temperature differences between bare soil and soil covered with llama dung.

Partitioning of plant material in tussock and also tiller of different length classes were tested against different compartments and years (2 years with contrasting precipitation) by 2-way ANOVA (log-transformed data) and posterior Tukey tests individually for the 2 different years. All statistics were calculated by R statistics, version 2.10.0 (R Development Core Team, 2009).

2.4 Results

2.4.1 Life conditions of *Festuca orthophylla* in the Bolivian Altiplano

Hourly air temperature varied between −15.4° (minimum) and +34.5° C (maximum; measurements from 2003–2008, a total of 1815 days). Air temperature fluctuated strongly between day and night; diurnal temperature amplitudes of more than 30 K were not exceptional (8% of all days in 2003–2008) and daily amplitudes lower than 15 K occurred in 10% of all days only. Annual mean air temperatures ranged between 6.8° and 7.1° C, the coolest month was June or July, and December usually was the warmest month (2004–2007; considering complete years only; Tab. 2.1). At the study site, total annual precipitation was 327 mm for the 2006–2007 rainy season, but rain started very late (highest monthly rain amount of 112 mm in March 2007). In the 2007–2008 season, highest precipitation per

month was observed in January (251 mm), and total rain amount was 384 mm (January to August 2008, Tab. 2.1).

Table 2.1: Air temperature and precipitation in Sajama (° C; Bolivian Altiplano, 4250 m a.s.l.).

Year	Precipitation	Air temperature			Coolest month	Warmest month
	(mm)	min	mean	max	(monthly mean)	(monthly mean)
2003[a]	n.a.[b]	−5.0[d]	8.2	31.0	Aug (4.4)	Dec (10.3)
2004	n.a.[b]	−10.3	7.1	32.6	Jun (2.7)	Dec (10.8)
2005	n.a.[b]	−11.9	6.8	34.5	Jun (2.6)	Nov (10.1)
2006	92.2[c]	−13.5	6.7	30.6	Jul (2.3)	Dec (10.7)
2007	321.3	−15.4	7.0	30.3	Jul (2.6)	Jan (9.5)
2008[a]	332.3	−14.1	5.6	28.2	Jun (2.9)	Feb (8.9)

[a] Temperature measurements did not cover the whole year in 2003 and 2008 (129 days for 2003 and 224 days for 2008, respectively).
[b] Rain data are not available (n.a.) for 2003–2005).
[c] Rain measurements started in May 2006 till August 2008).
[d] In 2003 the temperature sensor had lower limit at −5° C)

Temperature loggers in tussock and soil (−10 cm) registered cold and warm periods during almost two years (2006–2008). Daily minimum and daily mean temperature inside tussocks close to the leaf meristems were always warmer than daily minimum or mean air temperature (measured at 2.8 m above ground), whereas daily maximum temperatures inside tussocks was always lower than daily maximum air temperature. These differences were consistent across warm and cold seasons, although temperature differences between tussock and air were larger during warm seasons (Tab. 2.2, coldest and warmest months are listed). Around one quarter (24.3%) of all hourly temperature records (*ca.* 20000 values, 2006–2008, hourly data not shown) inside the tussock, *i.e.* close to the leaf meristems were below 6° C, a temperature often considered a threshold for tissue formation in plants. In contrast, 53.8% of all records (2006–2008) of air temperature were below this 6° C threshold. Air temperatures dropped below zero in 24.5% of all hourly records, whereas inside the base of the two tussocks such low temperatures were very rare (0.45% and 1.5% of all hourly records). Thus, leaf meristems experienced less harsh temperature conditions than measured for air temperature.

Uncovered ground is heating up strongly under full solar radiation, with daily minimum and mean soil temperatures (−10 cm) always higher than air temperature, but maximum soil temperatures at this depth were only slightly higher than air temperature during the warm season (Tab. 2.3). In contrast, during the cold (dry) season, daily maximum air temperature was consistently higher than the soil temperature maximum. Covering ground with llama dung hardly reduced day-time heating of soil (daily means and extremes were rather similar compared to bare soil).

The daily course of air temperature inside tussocks revealed that the upper part of the tussock (>35 cm above the soil in a 77 cm-tall tussock) was closely coupled to air temperature, whereas temperature in the tussock base paralleled the course of soil tem-

Table 2.2: Lowest, mean and highest air temperature (° C; in full shade at 2.80 m, 2006–2008) and lowest, mean and highest temperature within the *Festuca* tussock base (close to meristems).

Year	Season	Month	Air temperature			Tussock temperature		
			minimum	mean	maximum	minimum	mean	maximum
2006	dry	Jun	−7.3	2.7	16.3	1.1	4.7	7.8
	dry	Jul	−8.8	2.4	16.8	0.2	4.2	7.7
	rainy	Nov	−0.7	10.2	24.1	8.1	11.8	16.4
	rainy	Dec	0.4	10.8	24.2	9.1	12.8	17.3
2007	dry	Jun	-5.6	4.4	17.7	2.6	5.7	9.0
	dry	Jul	−6.8	2.6	15.1	1.0	4.2	7.8
	rainy	Nov	−3.4	8.5	22.3	6.9	10.9	15.7
	rainy	Dec	−1.2	9.4	22.5	8.1	11.3	15.0
2008	dry	Jun	−7.1	3.0	16.2	1.0	3.8	6.8
	dry	Jul	−7.8	3.0	16.8	0.8	3.9	7.1

perature (−10 cm) in open terrain but at a lower level (presumably because of shading by phytomass and litter; Fig. 2.2).

Volumetric soil moisture content (vol%) at 8–10 cm depth differed from zero only during the wet seasons, underpinning the extremely low soil water content in the uppermost 10 cm of these sandy, volcanic soils during the dry season. During the short rainy seasons, soil moisture tended to be slightly higher under tussocks than under open ground. Under tussocks, soil moisture reached a maximum of 5.5% and was on average 0.6% ± 1.1 (n = 62 days, n = 4 sensors; ± sd), while under bare soil the highest value was 1.5% and the mean 0.4% ± 0.4 (n = 62 days, n = 4 sensors; ± sd), reflecting the sandy texture. Soil moisture under open ground covered by llama dung was higher, even higher than near tussocks, with a mean of 7.3% ± 4.0 (n = 62 days, n = 4 sensors; ± sd), and a maximum record of 19.4%, indicating a strong mulching effect. Soil moisture under tussocks surrounded by llama dung did not differ significantly from control tussocks without dung, and averaged at 0.8% ± 0.8 (n = 62 days, n = 4; ± sd) with the highest value 3.9% after rain.

2.4.2 Light interception of *Festuca* tussocks

Light transmission declined exponentially, both vertically as well as horizontally (from top to base and from tussock periphery to centre). Only the outmost layer of 0.05 m and the uppermost 0.20 m in the tussock's centre experienced 75–100% of the incident light. This light zone 1 had 8% of the total phytomass, from which 67% was live. In the centre of tussocks, self-shading was considerable (Fig. 2.3). The innermost zone that contained 44% of the all phytomass (21% of which was biomass) received less than 10% of the incident light. While light decreased exponentially across the tussock canopy, the biomass fraction decreased from 67% in the outermost zone, to 21% in the innermost zone, but the absolute biomass in each zone was similar (54–110 g , Tab. 2.4). In canopy zones with less than 50% of the incident light, necromass significantly surpassed the biomass fraction. The

Table 2.3: Daily minimum, mean and maximum soil temperature (° C; −10 cm) under bare soil and under soil surface covered with llama dung (2006–2008).

Year	Season	Month	Soil temperature (−10 cm)			Soil temperature (−10 cm) with dung cover		
			minimum	mean	maximum	minimum	mean	maximum
2006	dry	Jun	1.0	5.7	11.8	–	–	–
	dry	Jul	0.0	5.2	12.1	–	–	–
	rainy	Nov	8.3	15.8	25.5	–	–	–
	rainy	Dec	9.9	16.9	26.6	–	–	–
2007	dry	Jun	3.1	7.1	12.0	2.4	6.6	11.7
	dry	Jul	1.7	5.9	11.1	0.8	5.4	11.4
	rainy	Nov	8.4	15.4	23.8	8.5	14.9	22.0
	rainy	Dec	9.4	15.1	22.1	9.8	14.4	19.6
2008	dry	Nov	1.8	5.7	11.0	–	–	–
	dry	Dec	1.6	6.2	12.3	–	–	–

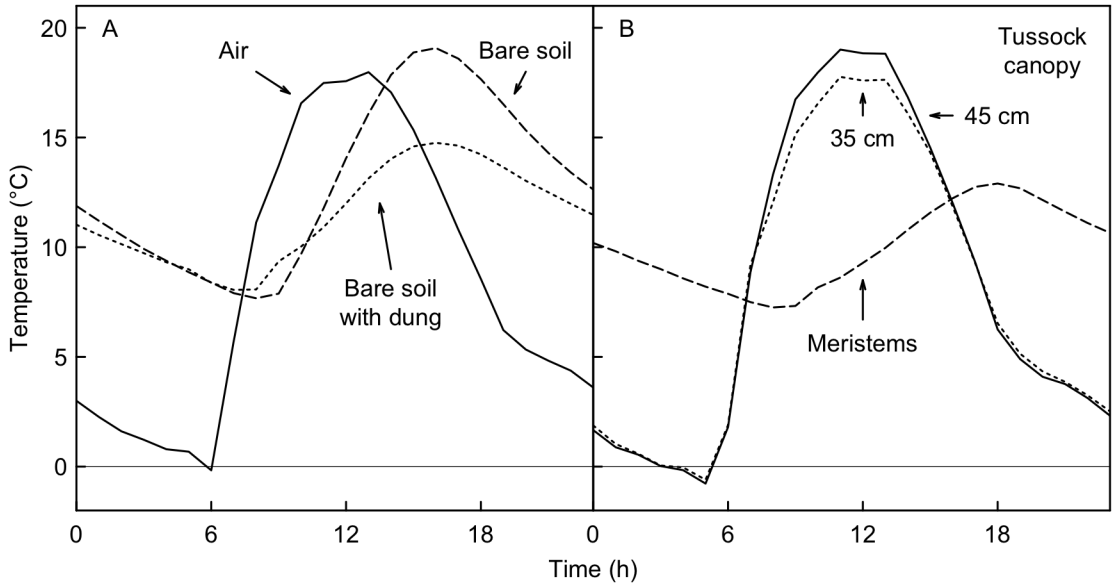

Figure 2.2: (A) Daily course of air temperature, soil temperature under bare soil and temperature of soil covered with llama dung (−10 cm). (B) Daily course of canopy temperature (45 and 35 cm above soil surface) and at the meristem level (base of the canopy, 5 cm above soil surface) within a 77 cm-tall *Festuca* tussock. Temperature readings were taken from 18 February to 5 March 2008.

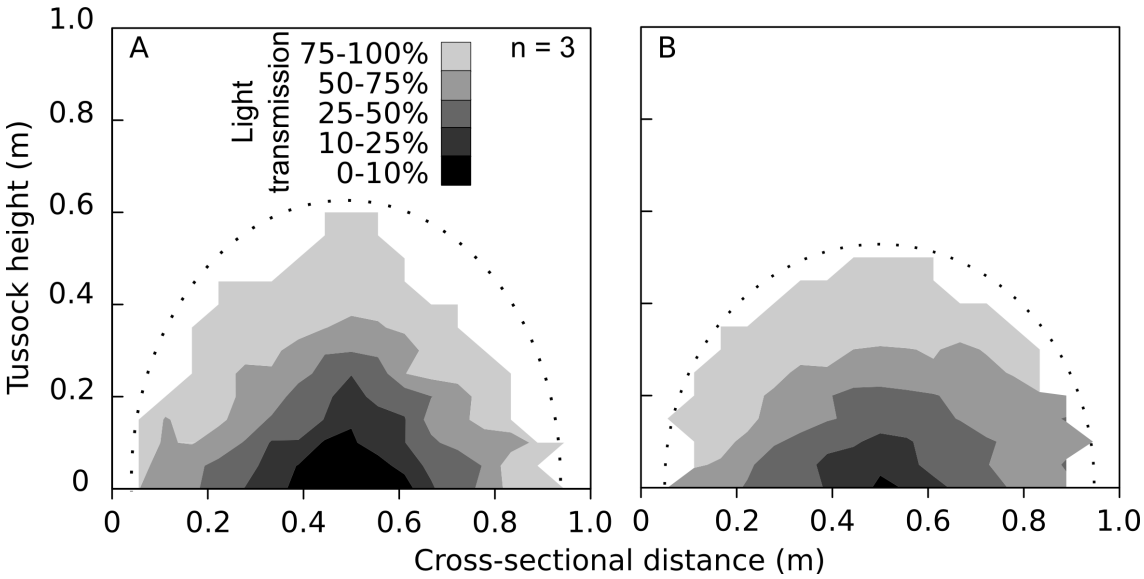

Figure 2.3: Light transmission zones (mean of 3 tussocks) in the *Festuca* canopies along two N-S profiles, one through the centre (A), and one parallel to the first at 15 cm from the centre (B).

fraction of senescent tillers was largest in zone 3 (<50% to 25% of light transmission).

2.4.3 Tussock morphology

From our measurements in 160 tussocks (whole plants as well as fragments) in an area of 132 m^2, we arrived at the following tussock characteristics. The frequency distribution of mean diameter (range 0.08–0.96 m) was left skewed (mean = 0.39, median = 0.37), with more than 60% of all plants (or fragments) having a mean diameter between 0.12 and 0.50 m and more than 70% of all tussocks had a height between 0.30 and 0.60 m. Tussock height increased linearly with tussock mean diameter up to a mean diameter of 0.50 m (no further increase in mean tussock height with diameter), although tussocks as high as 0.80 m occurred occasionally.

2.4.4 Tiller morphology

As is typical for tussock-forming grasses, tillers in *Festuca orthophylla* have extremely compressed internodes and shoot meristems remain below ground, *i.e.* everything seen above ground are leaf sheaths, leaf blades and inflorescences. The leaf sheaths form a tube and the new leaves formed by the basal meristem emerge through the interior of the leaf sheath of the second youngest, fully-expanded leaf in the same tiller (intravaginal tillering). Intravaginal tillering results in the compact life-form known as tussock, bunchgrass or caespitose grass, thus, it is impossible to distinguish a younger leaf of a mother tiller from the leaf of a daughter tiller produced simultaneously by the mother tiller. Therefore, it is impractical to use tillers as the monitored units in a long term, non-destructive study.

Table 2.4: Dry matter fractions in different 'light zones' of tussock canopies (n = 3, means ± sd)

Light transmission zone	Biomass (g)	Senescent (g)	Necromass (g)	Phytomass (g)
75–100%	110 ± 14 (67%)	17 ± 4 (10%)	38 ± 14 (23%)	165
50–75%	69 ± 20 (53%)	11 ± 3 (8%)	50 ± 21 (38%)	130
25–50%	54 ± 20 (39%)	16 ± 8 (11%)	71 ± 28 (50%)	141
10–25%	109 ± 26 (32%)[a]	14 ± 3 (4%)	214 ± 27 (64%)	337
0–10%	110 ± 25 (21%)[a]	35 ± 3 (7%)	378 ± 27 (72%)	523

[a] Increasing contribution of intravaginal leaf sheaths fractions ('stems')

Table 2.5: A morphometric characterization of *Festuca orthophylla* tussocks (mean ± sd).

Parameter (unit)	Value
Canopy diameter (m)	0.42 ± 0.10
Canopy height (m)	0.55 ± 0.10
Projected canopy area (m^2)	0.15 ± 0.07
Number of total tillers	3167 ± 1696
Number of live tillers	1896 ± 1380
Number of dead tillers	1271 ± 490
Number of live leaves (2008)	4335 ± 1603
Density of live tillers per tussock (tillers m^{-2})	13015 ± 5752
Density of live leaves per tussock (leaves m^{-2}; 2008)	23718 ± 9173
Above-ground phytomass (g)	854 ± 120
Biomass (g; 2007)	298 ± 114
Biomass (g; 2008)	493 ± 258
Necromass (g; 2007)	568 ± 200
Necromass (g; 2008)	354 ± 201
Intratussock litter (g)	318 ± 140
Total roots (g; 2007)	129 ± 63
Root-stock (g; 2007)	186 ± 125
Root sphere's radius (>projected canopy; cm)[a]	30

Total number of replicates n = 9, n = 3 for 2007 and n = 6 for 2008.
[a] Estimation of radial root extension beyond the projected canopy.

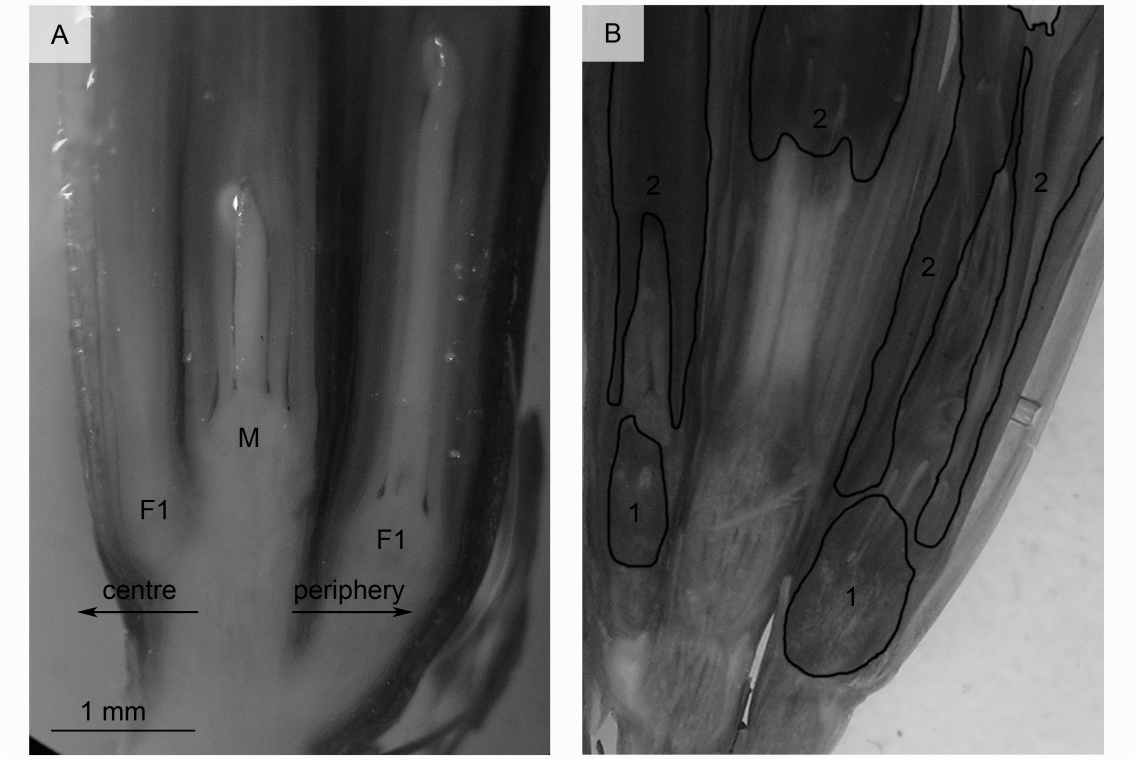

Figure 2.4: (A) Longitudinal sections through the basal part of ramets of *Festuca orthophylla* in the upper part of the root-stock. Mother tiller (M) at the centre and daughter tillers (F1) emerge at both sides (centrifugal and centripetal). (B) Zones of metabolic (meristematic) activity, stained by TTC.

The units that can be identified are the ramets, composed of one to several tillers, with their leaf sheaths and blades. We analysed many ramets containing one to several tillers, and found that, on average, one tiller has 2.9 ± 0.8 live leaves (mean ± sd; median = 3; n = 388 tillers). Hence, by dividing a tiller's number of live leaves by 2.9, we can roughly estimate the number of tillers within one ramet. These data were obtained from ramets collected in 5 randomly selected tussocks along 10 cm wide radial strips from the periphery to the centre of each tussock.

The longitudinal structure of whole ramet systems evidenced that tiller meristems have a below-ground position. Intravaginal tillering with hardly any internodal elongation leads to a very dense aggregation of shoots with almost no free space in between at the ground surface (Fig. 2.1). These longitudinal sections of ramets (Fig. 2.4A) also confirmed that tillering occurred not only centrifugally (towards the tussock edge), but also in other directions, including towards the tussock centre (although, less frequently). In Fig. 2.4B the pronounced red staining by TTC evidenced meristematic activity in both the apical region as well as in the leaf intercalary extension zones.

2.4.5 Tussock phytomass, biomass and intra-tussock litter

The selected nine tussocks had a mean projected canopy area of 0.15 m^2 and a mean above-ground phytomass of 854 g per tussock, which corresponds theoretically to nearly 6 kg m^{-2} tussock phytomass or 60 t ha^{-1}, if the landscape would be fully covered by such tussocks (no inter-tussock gaps). Above-ground biomass was 46% of above-ground phytomass (large amount of dead tillers, Tab. 2.5), and intra-tussock litter accumulated to nearly 300 g m^{-2} of tussock area (corresponding to 1/3 of above ground phytomass). *Festuca orthophylla* turned out to have a surprisingly shallow root system, since only very few roots grew deeper than 50 cm and hardly any roots at soil depth of 1 m (Fig. 2.1). Root-stock represented the major below-ground fraction (28% ± 6 of total phytomass), followed by roots <1 mm (14% ± 3) and roots >1 mm (7% ± 1, Figs. 2.1 and 2.5).

Tussocks harvested in the drought year (2007) had a lower biomass fraction of only 34% ± 3 (n = 3) of above-ground phytomass compared to a 58% ± 4 biomass fraction in a year with 'normal' rainfall regime (2008; n = 6, $P < 0.001$). However, the amount of intra-tussock litter that builds up over several years did not differ between the two years ($P = 0.428$, Fig. 2.5).

Biomass (live) fractions of tillers in different length classes varied between 2007 and 2008 (ANOVA, $P < 0.05$): in 2007 (dry), the biomass fraction decreased from 45% in tillers with a length between 20 and 30 cm to 36% in tillers exceeding 50 cm in tiller length. In 2008, the biomass fraction increased from 40% in tillers with a length between 10 and 20 cm to a fraction of almost 80% in tillers with length above 50 cm (Fig. 2.5). Hence, the dry conditions in 2007 largely reduced the green leaf fraction in large tillers but not in short tillers.

2.5 Discussion

Our field study in 4250 m elevation revealed a coherent picture of the structure and dry matter allocation in this dominant plant species of the Andean Altiplano. The above-ground phytomass accumulated in these *Festuca* tussocks is high by all standards. Even when accounting for the actual land cover by tussock canopies of only 13% (Chapter 3), the standing above-ground phytomass still averages at 0.850 kg m^{-2} (a number similar to the mean individual tussock phytomass by coincidence). Per unit tussock area, the dry matter density (6 kg m^{-2}) is exceeding that of a mature wheat field by a factor of *ca.* 5 and would rather match the phytomass of a 30 year old temperate forest. However, the 13% cover reduces the land area based means in phytomass. Our numbers are quite similar to those found in snow tussocks in New Zealand (*Chionochloa* sp.) with a phytomass between 0.18–1.18 kg per tussock (depending on tussock size), corresponding to a theoretical value of 8–13 kg m^{-2} at full cover, or 1.6–2.6 kg m^{-2} for the actual land cover of 20% (Williams, 1977). In an undisturbed area at the Colombian Páramos, the phytomass density at the landscape level (unknown cover, but close to full cover according to the author: "Some bare spots are present.") was smaller than in our site (0.464 *versus* 0.850 kg m^{-2}), but increased to >1.6 kg m^{-2} if the large amount of litter in that area is included (Hofstede et al., 1995*b*).

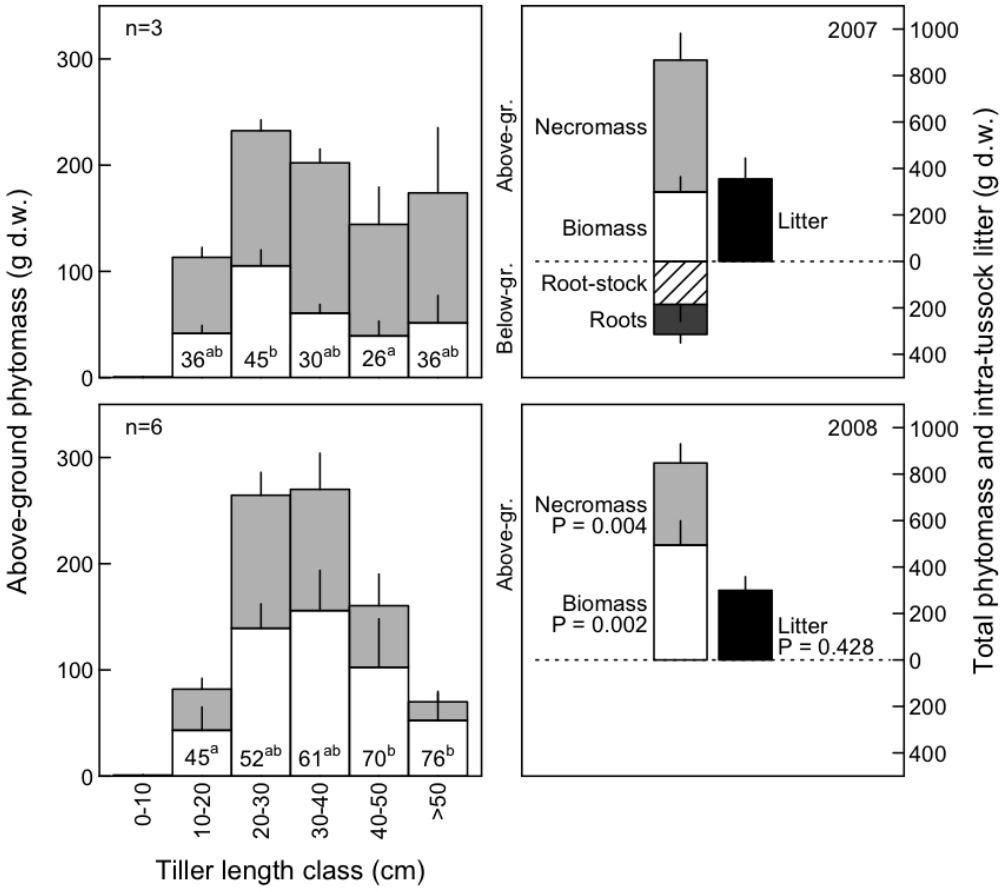

Figure 2.5: Dry matter partitioning in *Festuca orthophylla* tussocks (mean ± se). Left: contribution of different tiller size classes to total tussock mass (white: biomass and % values, grey: necromass). Biomass differed mainly between years ($P < 0.05$) and to lesser extent between tiller length classes ($P = 0.097$), leading to a highly significant interaction term 'year × length class' ($P < 0.001$). Right: mean tussock dry matter (dead and live) as well as litter (black). 2007 was an exceptional dry year, 2008 was a year with normal precipitation.

The most obvious feature of these tussocks is the large amount of standing dead biomass and litter (two fractions of dead material hard to separate in these plants, in our case 51% of all above-ground dry matter, excluding litter, is necromass). A high necromass and intra-tussock litter is rather characteristic for all tussock graminoids (Grabherr et al., 1978; Hnatiuk, 1978; Hofstede et al., 1995*a*; Mark, 1992; Meurk, 1978; Rehder, 1976; Williams, 1977). Necromass (*i.e.* disregarding litter) ranged from 46 to 83% of above-ground phytomass in other tussock dominated systems (Hofstede et al., 1995*b*; Meurk, 1978; Williams, 1977). In the Colombian Páramos, intra-tussock litter amounted to 18–265% of the dry matter contained in phytomass (but by definition litter is not included in phytomass). This dry matter pool might be reduced by disturbances such as grazing and burning (Hofstede et al., 1995*b*). Dry conditions (cf. drought year 2007) may shift the biomass to a larger necromass fraction, but our data indicate that this is due to a reduced green fraction and only a slight an increase in necromass in absolute terms.

A large accumulation of dead plant material reflects low rates of decomposition, explains the high phytomass density per unit ground area, affects microclimate (Körner, 1982) and makes this ecosystem fire prone. In *Festuca orthophylla* the large amount of sharp, standing dead foliage may also exert some herbivore defense (a sort of cactus syndrome), or at least dilutes spatially the quality of fodder per bite. The obvious trade-off is a significant contribution to light interception and thus shading of green foliage as illustrated by the light profiles obtained. It really is the green part at the periphery that captures most solar radiation, a part of the canopy that does not profit from microclimatic shelter and is most exposed to herbivores.

While below-ground biomass commonly exceeds above-ground biomass in the majority of grasslands in semi-arid and arid regions, *Festuca orthophylla* has a smaller or similar below-ground than above-ground biomass fraction. Since much of the root-stock is in fact stubble mass, which is functionally belonging to above ground plant mass (Körner, 2004), the 'true' below ground fraction becomes even smaller. Expressed as root mass fraction (RMF of 21%, roots in % of total plant biomass) *Festuca orthophylla* clearly ranks below (excluding the root-stock) the range of root mass fractions reported for high elevation herbaceous plant species worldwide (around 30%; Körner, 2003). RMF in co-occurring inter-tussock herbaceous species averaged at 54% (48% in tap roots, 6% in fine roots) at our field site (Patty et al., 2010). Since we could not separate dead, fine roots, this may be a conservative estimate of RMF in *Festuca*. Tussocks in the wetter regions of the Colombian Páramos (Hofstede and Rossenaar, 1995) and also in lowland sub-antarctic Islands (Jenkin and Ashton, 1970; Meurk, 1978) showed higher below-ground than above-ground biomass fractions. Unfortunately, none of these authors separated roots from root-stock (or specified this). Yet, the rather special position of *Festuca orthophylla* is retained, even when the root-stock was included in those previous works. Generally, it is believed that biomass allocation shifts from a dominance of shoots to a dominance of roots across different habitats as soil resources become scarce (Mokany et al., 2006), and alpine plants make no exception (Körner, 2008; Körner and Renhardt, 1987).

Digging to 1 m soil depth at the study site revealed that the majority of roots ends at soil depth between 30 and 40 cm and hardly any roots are found below, as is typical for cold, seasonal climates of the temperate zone (Körner, 2003). *Festuca* tussocks seem

to control their tissue water relations mainly by horizontal spacing of individuals (*i.e.* via leaf area index; Geyger, 1985). Distances between single tussocks were rather pronouced, yielding a canopy cover of only 15% (Chapter 3). Our soil moisture data also suggested a slower desiccation (and/or an attraction of rainfall) under Festuca tussocks than in the fully sunlit inter-tussock space (substantial radiative heating during the day). The *Festuca* root sphere extends *ca.* 30 cm beyond the tussock's above-ground periphery, which leads to an approximatively six times larger ground occupation by roots compared to projected tussock area. The root spheres of neighbour tussocks mostly do not overlap (personal observation by E. Hiltbrunner). Hence, each tussock takes advantage of about six times the rain fall calculated per unit of tussock canopy area, partly explaining why these tussocks tolerate long dry periods and keep producing new leaves into the dry season (Chapter 4). Tussock spacing is indeed key to understand tussock water relations in this dry environment (Geyger, 1985). A shallow, widely spread root system (as is commonly formed by succulents) permits efficient capture of small and ephemeral rainfall events, with the sandy soil permitting rapid percolation (Ursino, 2009). A similarly shallow root system was found in *Festuca pallescens* in a semi-arid Patagonian grassland at 1160 m a.s.l. (290 mm annual precipitation), more than 70% of the roots were in soil depth of 0–30 cm. However, a few roots were found to reach soil depth of 2 m, thus, had access to additional soil moisture of deep soil layers (Schulze et al., 1996), not what we observed here.

Intensive grazing by camelids and regular burning under the given rather harsh climatic conditions may have contributed to this reduced below-ground allocation in *Festuca* at the study site. Under heavy grazing, below-ground biomass was significantly lower than when cattle was excluded for 30 years in a semi-arid grassland of Mongolia (Gao et al., 2008). Repeated removal and resprouting of above-ground shoots most likely reduces root biomass in the longer term. However, in most grassland ecosystems with locally adapted grazing regimes, grazing does not seem to affect below-ground productivity (Milchunas and Lauenroth, 1993; Thorne and Frank, 2009). On the other hand, only very few studies reported a stimulating effect of grazing on below-ground biomass under dry conditions (*e.g.* Pucheta et al., 2004). In grazed Páramos grassland with a higher precipitation (>900 mm), Hofstede and Rossenaar (1995) even observed an increase in below-ground allocation when grazing was superimposed by fire, but it is always hard to tell, whether such allocation ratios change due to greater root or reduced leaf mass.

Shoot meristems of *Festuca orthophylla* are nested in a dense envelope of leaf sheaths, and are located *ca.* 2 cm below the soil surface, and thus, are protected against grazing and possibly also against fire damage, and are well buffered against extreme daily variations in temperature. The insulation of the meristematic zone against freezing temperatures in tussocks was already documented for the afro-alpine zone (Hedberg, 1964). Of all plant life forms at high elevation, tussocks seem to be the least efficient in terms of capturing solar heat around their photosynthetically active parts (Körner and Cochrane, 1983). With their open green canopy and narrow foliage, the majority of leaves operate near air temperature, while the centre is occluded with debris that insulates the root-stock and the meristems therein from both, radiative warming and cooling. The net outcome is cool foliage (close to air temperature) and a moderately warmer, almost frost-free growing zone. Given the well known marginal effects of temperature on photosynthesis in alpine graminoids

(Körner, 1982) and the low temperature optima in tussocks, but the high sensitivity to low temperature of meristems (Körner, 2003), the negligible thermal benefits in the leaf canopy do not appear to exert a major drawback. Cushion plants, with their peripheral meristems have been described to trap heat much more efficiently and differences between canopy and air temperatures in the range of 10–20 K have been observed repeatedly (Cavieres et al., 2006; Gauslaa, 1984; Körner and Cochrane, 1983; Körner, 2003). Such microclimatic modifications by cushion plants can enhance the establishment and survival of other plant species, graminoids in particular (facilitation; Cavieres et al., 2007) and even the performance of insects (Molina-Montenegro et al., 2006). However, leaf temperatures at the surface of *Azorella compacta*, an abundant, solid, mega-cushion species in the semi-arid Altiplano, occasionally co-occurring with *Festuca orthophylla*, followed more or less air temperature during the day, which is only possible through either massive evaporative cooling or rapid dissipation of heat to the woody socket of these tussocks – an unanswered question (Kleier and Rundel, 2004).

The high degree of self-shading adds to the low fraction of biomass in the lower part of these tall tussocks. Using leaf number, leaf width and leaf dry matter, we estimated a green area index per tussock (GAI, green parts only, one-sized projected area) of *ca.* 2 m^2 m^{-2}, which is very close to that reported for mats of *Carex curvula* tussocks in the Alps (Körner, 1982). Expanded to a landscape scale, the GAI would be around 0.25 m^2 m^{-2}. Such low GAI (except for inflorescences a synonym for LAI) values were reported for heavily grazed, semi-arid grassland in the Inner Mongolia (Fan et al., 2009).

Finally, the meristem position *ca.* 2 cm below-ground surface in combination with insulating, dead leaf sheaths is very common among grasses in fire prone regions (Choczynska and Johnson, 2009; Gibson, 2009). As exemplified by *Calamagrostis* tussocks, burning causes temperatures of >500° C in the upper grass canopy whereas the temperature at 2 cm below the ground never exceeded 65° C (Ramsay and Oxley, 1996). Pelaez et al. (2003) demonstrated that the response of tussocks to fire is species-specific in semi-arid Argentinean grassland at low elevation. In *Festuca orthophylla* vulnerability to fire also seems to be age dependent, because fragmented tussocks are more affected than intact tussocks (unpublished data), perhaps due to higher necromass fractions and thus, longer fire residence time.

In conclusion, our data provide a quantitative characterisation of the architecture and dry matter investment of this dominant Altiplano species. In a number of ways the traits exhibited, contrast *Festuca orthophylla* from other, non-woody, high elevation taxa. In particular, the foliage of these tussocks operates at temperature close to that of the free atmosphere, while at the same time, providing shelter to below-ground shoot meristems. The roughly 6-times larger extent of the root-covered area compared to canopy area, indicates access, at least for certain periods, to six-fold rates of precipitation, thus illustrating the significance of plant spacing in such semi-arid regions. The large amount of dead plant material constrains photosynthetic light interception, and reflects slow rates of decomposition, a likely trade-off of generally poor nutrional quality (Patty et al., 2010), which, in turn, relates to the heavy herbivory pressure. These tussocks appear to invest and prioritize in traits related to longevity and defence over those related to high productivity. Current land use practices, such as frequent burning and over-grazing by camelids are

likely to weaken this dominant high Andean plant and further constrain its contribution to sustainable livelihood.

3.0 Biomass production of tall tussock grassland in the Andean Altiplano

3.1 Abstract

Primary plant production is unknown for tropical mountains, since the classical harvest method cannot be applied under conditions of continuous growth without interfering with growth. With a non-destructive method, based on the number of leaves produced per ramet, length to weight ratios of leaves, ramet density within tussocks, birth, growth and death of leaves in ramets and land cover by tussocks, we estimated the primary production per total land area in the Bolivian Altiplano (4250 m a.s.l.). The dominant species in this area is *Festuca orthophylla*, forming tall tussocks. Above ground annual biomass production accumulated to *ca.* 1 kg m^{-2} in both, a relatively dry and a normal year, hence the difference in precipitation (327 mm *vs.* 384 mm) had a relatively minor effect. Fencing out camelids increased the above-ground production of undamaged ramets. The application of llama dung combined with animal exclusion increased the biomass production by 64% in the dry season of the first year. New leaves emerged throughout the year, hence there was no period of complete inactivity despite the 7–8 month rainless period. Ramet mortality (associated with ramet turnover and, thus, new ramet production) was higher during the rainy season, and fencing reduced mortality during the dry season, but not during the rainy season. Fencing also had no effect on flowering, but clipping and fire suppressed flowering. New root arrival in in-growth cores made up *ca.* 19% $\pm$ 5 of the original root biomass per unit ground area. Llama dung addition did not affect, but fire reduced the root production in in-growth cores. The large root spheres of *Festuca orthophylla* tussocks most likely compensate for the low rates of precipitation per tussock canopy area. The resultant continuation of leaf production despite strong moisture seasonality explains why *F. orthophylla* provides year-round renewed forage for camelids in this semi-arid high mountain ecosystem.

3.2 Introduction

High elevation grassland productivity is only known for temperate mountains. Data for the tropics are missing, because the classical seasonal harvesting technique does not work for tropical perennial plants (Körner, 2003). With year-round growth, it is impossible to separate the phytomass that was already present at the beginning of the study from the

phytomass produced during the study. In the temperate zone, alpine grassland produces 200–300 g m^{-2} of above ground biomass per land area in a 2–3 month growing season (Körner, 2003); in a 12 months tropical climate, we would thus expect *ca.* 1200 g m^{-2}, provided adequate moisture and nutrient availability.

In the maritime temperate zone, tussocks of the genera *Chionochloa* with close to year-round activity in lower montane New Zealand, exert a lot of morphological similarities to Andean tropical tussocks (*e.g.* tall tussocks with high standing necromass and intra-tussock litter content (Mark et al., 2000), and their leaf elongation rates have been suggested to be in the same range as in the tropics (Hofstede et al., 1995*a*; Mark, 1965). Williams (1977) developed a non-destructive method to estimate the above-ground net biomass production of a *Chionochloa* tussock grassland in New Zealand, based on the length of new leaves produced per tiller in a season, the weight to length ratio of leaves, and the tiller density in the landscape. He arrived at 330 g m^{-2} a^{-1} for *Chionochloa macra* and 518 g m^{-2} a^{-1} for *Chionochloa rigida* per total land area, for a growing season of 7.5 months of 'normal' growing conditions in areas with an average tussock basal area of 20% of the landscape. If we assume that the tussock canopy area is 2–3 times larger than the tussock basal area (the area covered by tillers at ground level), actual cover by tussocks could be extrapolated to 40–60%, an extrapolation to full ground cover would theoretically arrive at a 600–1550 g m^{-2} a^{-1} above ground biomass accumulation. A similar approach resulted in 550 g m^{-2} a^{-1} (over a 256 day season) for *C. ririda*, 628–834 g m^{-2} a^{-1} (two sites over a 148–228 day season) for *C. macra*, and 843 g m^{-2} a^{-1} per total land area (over 219 days) in a region with a co-dominance of both species (Meurk, 1978) and land cover ranging from 23–83% (assuming that the author refers to tussock basal area instead of projected canopy area, but there is no definition), once more yielding rather high productivity when scaled to 100% ground cover.

In the tropics and sub-tropics, Ramsay and Oxley (2001) estimated an above ground biomass production of 430–512 g m^{-2} a^{-1} for *Calamagrostis intermedia* in the year-round wet part of the Ecuadorian Andes by repeated harvesting. However, re-growth after clipping may lead to unknown treatment effects (lack of mutual shading by dead parts, compensatory growth, altered water regime). The above ground productivity estimates per total land area by Hofstede et al. (1995*a*) in Colombian Páramos rangeland (again with *Calamagrostis intermedia*) resulted in only 198 ± 74 g m^{-2} a^{-1}, 1/6 of what might have been expected from extrapolating temperate latitude alpine grassland productivity to a 12 months growing season. Estimates for *Deschampsia klosii* tussocks at Mt. Wilhelm in New Guinea, again with a year-round wet growing season, arrived at 128–442 g m^{-2} a^{-1} per total land area (data for 6 locations; Hnatiuk, 1978). In these last two studies, assessments combined leaf elongation rates with length to weight ratios and leaf density data, but none of these studies accounted for leaf emergence rate, assuming that all leaves were growing continuously and that leaves were substituted by a new growing leaf immediately after they had completed expansion. This could have incurred large errors in biomass production. These numbers are quite low, perhaps owing to the low dose of solar radiation in these almost permanently cloudy environments. Overall, there are no data for biomass production for such tropical high elevation grasslands that do reflect undisturbed rates of biomass production and, thus, could be compared with data from mountains in the

temperate zone. The lack of reasonable scaling from tussock-specific to land area-specific productivity may have three reasons: (1) Tussocks intercept far more light than one might expect from their actual ground cover, (2) ground cover is hard to define given the diffuse boundaries of individual tussocks (basal area represents a massive underestimation of cover), and (3) the root spheres of tussocks (and, thus, their access to ground moisture and nutrients) is several times that of canopy ground coverage, hence it may arrive at close to 100% soil exploration in tussock grasslands as dense as those in New Zealand. Quite obviously, cover definitions impact the comparability of data and deserve particular attention.

Festuca orthophylla is a tall tussock-forming grass that covers large rangeland areas in the subtropical- and tropical-Andean Altiplano between 3600 and 4680 m a.s.l., largely around 4000 m (Chapter 2). It is the only dominant species in the dry pajonales, eventually sharing space with shrubs of the genera *Bacharis* and *Parastrephia*. Small annual and perennial herbs only emerge during the rainy season of the austral summer. These inter- and intra-tussock herbs contribute very little to biomass, but often have a high nitrogen concentration (Patty et al., 2010). Yet, *Festuca orthophylla* represents the dominant component of the biomass, key to the primary production of this ecosystem on which traditional camelid husbandry depends. Whether the absence of woody species is natural or anthropogenic is not resolved (Ellenberg, 1996; Hammen and Cleef, 1986; Wesche et al., 2008), and if there is any natural limitation for the presence of trees, it certainly is not temperature, since *Polylepis tarapacana* grows well several hundred meters above the grassland plains (Hoch and Körner, 2005). Recurrent fire selects for plants with belowground meristems and rapid re-growth potential after fire, and may be the cause of a shift from woodland to tussock grassland (Spehn et al., 2006). Currently, our study area is probably free of natural fire, perhaps due to the wide spacing of tussocks. Fire hardly jumps from tussock to tussock, except under very strong wind (personal observations by the first author). Burning old tussocks is the only traditional management, which aims at eliminating standing dead material (also intra-tussock litter), facilitating nutrient recycling. However, neither the re-growth of burnt individuals of *Festuca orthophylla*, nor the impact of grazing on post-fire re-growth were ever studied. A spreading of llama dung from overnight kraals may improve soil nutrient availability and soil moisture retention, but this technique had not been applied, and neither had the possible effect of llama dung addition on the vegetation been explored.

Livestock management has a very long tradition in the Bolivian Altiplano, with peak activity dating back to the XI and XII centuries in the Inca Empire (Cardozo, 2007). This long-term plant-animal interaction may have promoted *F. orthophylla* due to its fire and grazing resistance, and may have led to an equilibrium with the husbandry system for centuries. However, changes in the economy of the macro-region offered possibilities to the livestock owners to increase the income by working in the city and buying more animals, exceeding the rangelands' carrying capacity. Therefore, it is very important to know the productivity of the dominant species *Festuca orthophylla*, also as a first step towards estimating its carrying capacity for sustainable land use. Accordingly, we asked the following questions: (1) What is the annual biomass production of *Festuca orthophylla*? (2) Is there any compensatory growth in response to grazing? (3) How is

biomass production responding to burning, clipping, or the addition of llama dung?

In addition, the study covered plant responses for the dry and the rainy season over two complete years, a drier and a more normal one, thus, offering the possibility to evaluate the impact of water shortage on biomass production. We fenced four parcels of the experimental area to exclude llamas and alpacas to test the fencing effect and additional management treatments in a nested design (llama dung addition, clipping and fire).

3.3 Material and methods

3.3.1 Study area

The Sajama National Park in western Bolivia is close to the border to Chile (S 18° 08' W 68° 58' at 4250 m a.s.l.) at the western limit of the Andean Altiplano. Vast, flat valleys, surrounded by volcanoes, characterize the landscape. At the valley level there are two main ecosystems: The bofedales close to riverbeds, are wet and have a dense cover of short-stature vegetation (tussocks are rather rare); the pajonales, well drained and thus dry (sandy volvanic soil), one to few meters above rivers and pounds, with a sparse plant cover and the dominance of *Festuca orthophylla* tall tussocks.

The climate is characterized by seasonal precipitation. Most of the rainfall occurs between November and March, with a peak in January and February, and the annual precipitation is 300–350 mm (Hardy et al., 1998). Year-round air temperatures are low and the diurnal amplitude is greater than the amplitude between summer and winter (8.6% of the days show an amplitude in air temperature of even more than 30 K; 2003–2008), with means of air temperature of 2.3° and 10.7° C for the coldest and warmest month (Chapter 2).

We selected 8 parcels of 25 × 25 m in a pajonal site, 4 were fenced and 4 left non-fenced, each pair of fenced and non-fenced parcels were considered a block. The fences were made of 2 m posts and wire, up to 1.35 m height. Each fenced or non-fenced parcel was subdivided into 4 equal subplots, one subplot served as control, the second received 400 L of dry llama and alpaca dung every year, at the beginning of the dry season (April 2006 and May 2007). In the third subplot the studied plants were clipped in May 2006 at a height of 10–15 cm above the ground (*i.e.* below the ear of the lowermost leaves, all leaf blades removed). The fourth subplot was artificially burnt in April 2006. In each subplot, six tussocks were selected to test the interaction of fencing and the other treatments on tussock growth.

3.3.2 Leaf and ramet census

Our production assessment was based on counting ramets (density), emergence and elongation of new leaves in marked ramets and length mass ratios as described below. A tiller of *Festuca orthophylla* consists of a main basal meristem, the respective leaves with leaf sheaths and the inflorescence, which also commonly terminates a tiller's life (Chapter 2). Tussocks or bunchgrasses are characterized by very compact growth form, resulting from intravaginal tillering. For this reason it is impossible to distinguish between new leaves

belonging to the originally marked tiller, and the first leaf of a daughter tiller that emerged intravaginally. A higher level of organization is the ramet, a collection of closely interconnected tillers, capable in living independently (Silvertown et al., 1993). Therefore, we adopted ramet as the lowest organizational level of the tussock. We will refer to 'ramet' in the production assessment, irrespective of how many tillers a ramet contains. Since both ramets and tillers consist of a minute below-ground stem section with apical meristems, tillers and ramets in essence represent leaves consisting of leaf sheaths and leaf blades. A stem is only formed when tillers flower, followed by their death. In other words, the above-ground dry matter of tussocks consists of foliage and inflorescences. Tussock area is defined here as the ground area under the vertical projection of the tussock's crown (the tussock base covers a much smaller area). Roots, on average, expand *ca.* 30 cm beyond the tussock ground area as defined above, thus, root spheres cover an area substantially larger than the tussock area, but tussocks in this grassland are widely spaced so that root spheres hardly overlap.

The biomass of leaves produced between two census dates was assumed to represent ramet biomass gain. We converted leaf number and leaf length data into biomass increments by attributing a leaf length/weight ratio obtained from 311 ramets of 8 tussocks selected within a random 10 m transect. Within a given tussock, we harvested a radial strip (periphery to centre) in order to include different ramet states. Because of intravaginal tillering, we sometimes observed ramets with two simultaneously growing leaves. Since such ramets were quite rare, they were discarded to simplify the model. For each ramet, we measured the length and weighed each of its leaves separately (leaf sheath + leaf blade). Since the length of the longest leaf correlated with the mean length of all leaves in a ramet, irrespective of the number of leaves, we used the length of the longest leaf as a proxy of the cumulative length of leaves in each ramet (number of new leaves $\times$ mean length = cumulative length of all leaves). Therefore, the cumulative length of new leaves produced in each season could be calculated from the length of the longest leaf.

3.3.3 Tussock land cover

Tussock land cover was assessed using images taken with a digital camera (Panasonic Lumix DMC FX-12) hanging from a 12 m fiberglass telescope pole (Spiderbeam Antennas, Germany). These pictures were taken from a 9 $\times$ 9 m area in each of the subplots of 12.5 $\times$ 12.5 m, after placing a 3 m grid of yellow plastic tape across the area, with a 1.10 m reference stick. The pictures were merged using the yellow tape grid as a reference. Furthermore, we distributed randomly and virtually 14 transects of 10 m length over each image and measured the land cover by the line-intercept method (Bonham, 1989). Since these were color images, we also could separate live and dead tussock parts, recording fragmented parts of tussocks separately, and avoiding dead zones of older clonal clusters. This land cover assessment was done only once, and images were taken in the dry season of 2007 (August-September) and 2008 (June).

In a second approach, we used a 10 m long wire randomly stretched over (and 'through') the tussocks at 30 cm above the ground (25 transects in the area around our experimental plots), again using the line-intercept method.

3.3.4 Ramet demography

To calculate the dry matter production per total land area, we assessed leaf production of ramets by regular censuses. In each subplot, we marked 5 ramets in each of 6 randomly selected, representative tussocks. Ramets found dead or lost by the time of revisitation were immediately substituted by new ones. The ramets were taken from different positions between the periphery and the centre of a given tussock. All ramets were labelled on May 2006 and then revisited on October/November 2006, March/April 2007, September/October 2007 and March/April 2008, *i.e.* at the end of each rainy and dry seasons. Though most precipitation occurred in January and February, we defined the rainy season as the period starting with the first rain event (generally in October-November), to the last precipitation of the season (March-April). We measured maximum ramet length (*i.e.* longest leaf length, from ground level to leaf's tip). Ground level was defined as the tussock's solid base, which is somewhat higher than the surrounding bare ground surface (Chapter 2). At each census, we observed the number and state of leaves (green, senescent, dead), as well as the ramet life-stage (vegetative, reproductive or dead). Ramet mortality and flowering were calculated in each census as the fraction of marked ramets per studied tussock that died or flowered at the respective season. Since ramets are monocarpic, *i.e.* die after flowering, ramet mortality can be divided into ramets that died without flowering, and ramets that died after flowering. We pooled mortality irrespective of its cause. The grazing impact was assessed in non-fenced areas as the percentage of marked ramets per studied tussocks that showed traces of grazing between two consecutive censuses (*i.e.* missing leaf tips).

3.3.5 Above-ground primary production

Production was estimated, combining the ramet census data with the leaf weight per leaf length relationship, scaling to total land area by using the land cover data and the ramet density per tussock area (Chapter 2). We avoid the pretentious term NPP (net primary production) because, as defined by Boysen-Jensen (1932), it cannot be assessed in the field (gross primary production minus all respiratory and exudation losses). So, what we present here is annual biomass accumulation.

From the length of the longest leaf in each ramet we calculated by linear regression analysis the mean length of all new leaves produced per ramet per season. Then, using the leaf weight per leaf length relationship, we calculated the mean weight of all leaves produced on a ramet between two censuses, and multiplying this result by the number of leaves produced in this period, we obtained the biomass increments of ramets over that time period. Further, we multiplied the ramet density per projected tussock area (median = 10,000 ramets per m^{-2} tussock, n = 9 tussocks, unpublished data from Chapter 2) by the tussock cover taken from aerial photographs in each subplot to calculate the ramet density in each subplot on a total land area basis. By multiplying the ramet density by ramet biomass increment, we assessed the production per total land area in each subplot for a given season. We did not treat inflorescence production separately, but rather assumed that inflorescences were produced from biomass (non-structural carbohydrates)

simultaneously re-allocated from senescing leaves of the given ramet.

$$Foliage\ production = ramet\ biomass\ increment \times ramet\ density\ per\ tussock\ projected\ area \times tussock\ land\ cover$$

3.3.6 Root biomass and root production

It is near to impossible to assess roots in the massive rootstock below the tussock, but the roots radiating from the tussock base can easily be sampled by soil coring. Since sequential coring in a steady state system cannot be converted to a measure of root production, we applied a modified in-growth core method to arrive at least at a proxy for rates of new root growth in response to our treatments. Thus, we re-sampled defined boreholes which were filled with sieved soil (root free) from the same borehole from which initial fine root biomass was obtained. The initial boreholes were marked with a PVC ring buried to a depth of 2 cm.

We cored the soil with soil corer; the iron tube of the corer fitted exactly inside a PVC tube (30 cm long), that was left in the hole while harvesting the soil cylinder, preventing the hole from collapsing (sandy soil). We cored 4 cylinders near each of the 3 tussocks in each subplot, 15 cm from the tussock base, avoiding the vicinity of obviously dead sectors of tussocks. Because of camelid trampling damage to our marker rings, we restricted the in-growth core measurements to the fenced plots. During the first campaign the core's cross-sectional area was 69.0 cm^2 (9.4 cm in diameter), and for re-coring (July 2008, *i.e.* 17 month after the first coring) we used a tube with a smaller cross-sectional area (47.4 cm^2, 7.8 cm in diameter) to ensure that we core only the root-free space left from the first core. Roots were sorted out from soil cores with tweezers, and dried to constant weight at 80° C before weighing. We estimated the root mass per total land area using the data for root mass fraction (root mass as a fraction of total tussock biomass) and total tussock biomass per tussock canopy area (Chapter 2), and scaled these data to the landscape level using total tussock land cover as obtained in this study. Root turnover was calculated by dividing the new root mass per core by the initial root mass per core area. We scaled the 17-month period to a 12-month growing season. This relative number for new root arrival in boreholes is considered a proxy for the response of root growth to our treatments. In the absence of overall root production data, these in-growth core data also offer at least a rough idea of the magnitude of root vigor in this environment.

3.3.7 Statistics

The tussock land cover was analyzed with a generalized linear model (glm) and arcsin-transformed values, with fixed factors fence and treatment nested in fence. The relationship of tiller length to mean leaf length was analyzed with a linear regression of $\log_{10}$ transformed values (n = 309, 2 outliers removed). For the leaf length to weight relationship, only length was transformed ($\log_{10}$; n = 308, 3 outliers removed). Biomass production was analyzed using a repeated measurements generalized linear model. Each season was analyzed separately using a generalized linear model. The data for biomass production were $\log_{10}$ transformed, the fixed factors were fence, and treatments nested in

fence. In non-fenced plots, ramets that have lost leaves or had severe traces of grazing (reduction in length) were removed from the analysis. Since the number of marked ramets per tussock varied due to losses, the values for ramets were averaged for tussock, and the tussock was the unity of the analysis.

The amount of roots harvested in the first coring campaign ($\log_{10}$ transformed) and the percentage of new root growing in the in-growth cores (arc-sin transformed) were analyzed with analysis of variance, with treatment as fixed factor. The 4 cores for each tussock were averaged, and the replicated unit was the tussock.

Ramet mortality, flowering and grazing impact were assessed as the percentage of ramets per tussock dyeing, flowering or showing traces of grazing at each census. Mortality and flowering were analyzed with a repeated measurements generalized linear model, with fence and treatments nested in fence as fixed factors. Since the grazing impact was analyzed only in non-fenced subplots, the repeated measurements generalized linear model used had only treatments as fixed factors. The 4 periods were analyzed separately.

3.4 Results

3.4.1 Leaf biometrics

Each tiller had 2.99 green leaves. The length of the longest leaf, scaled linearly with the mean length of all leaves per ramet, following the equation: $log_{10}(meanleaflength) = -0.103 + 1.304 \times log_{10}(lengthoflongestleaf)$ ($r^2 = 0.953$; Fig. 3.1). Mean leaf wight was obtained from mean leaf length per ramet by the linear regression: $(meanleafweight) = -0.160 + 0.159 \times log_{10}(mean\ leaf\ length)$ ($r^2 = 0.733$; Fig. 3.1). Across tussocks, mean leaf length above ground level was 27.6 cm (median 25.0 cm), with a distribution slightly shifted to the left.

3.4.2 Above-ground biomass production

The annual biomass production (summing up the means for the dry and subsequent rainy season) was 1000 g m^{-2} during the first drier year, and 1016 g m^{-2} for the second studied year (non-fenced control subplots, Table 3.1 and Fig. 3.2). Except for one non-significant instance (second rainy season), fencing always enhanced the biomass production (Tables 3.2 and 3.3). Treatment specific effects of fencing were largest in fire treatments, but also substantive in dung during the first dry season (fenced dung vs. non-fended dung). Within fenced subplots, clipping reduced the biomass production in the first dry season, but increased the biomass production in the subsequent rainy season (Supplementary Table 6.1).

Multivariate tests underline that fencing had an overarching significant effect, also interacting with treatments, but not with seasons (Table 3.2). Univariate repeated measurements tests (Table 3.2) showed significant effects of both, fencing and treatments, except for the last rainy season. These effects are strongly influenced by the fire effect, which had the greatest benefit of fencing (camelids removing most re-growth in non-fenced fire).

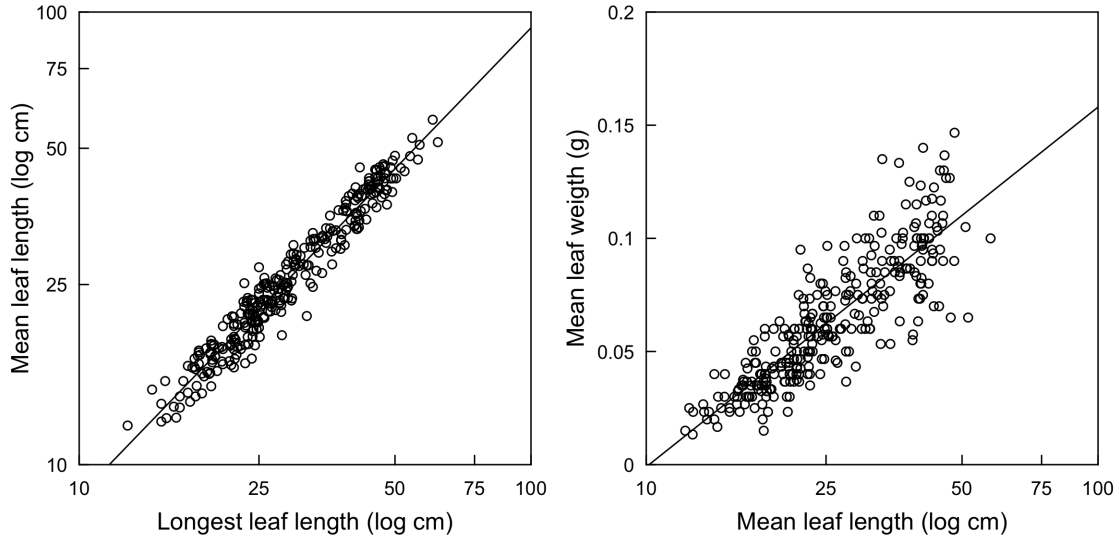

Figure 3.1: Linear correlation of the mean leaf length with the length of the longest leaf (left panel) and linear correlation of the mean leaf weight with the mean leaf length (right panel). Sample size = 311 tillers, harvested from 8 tussocks at a random transect.

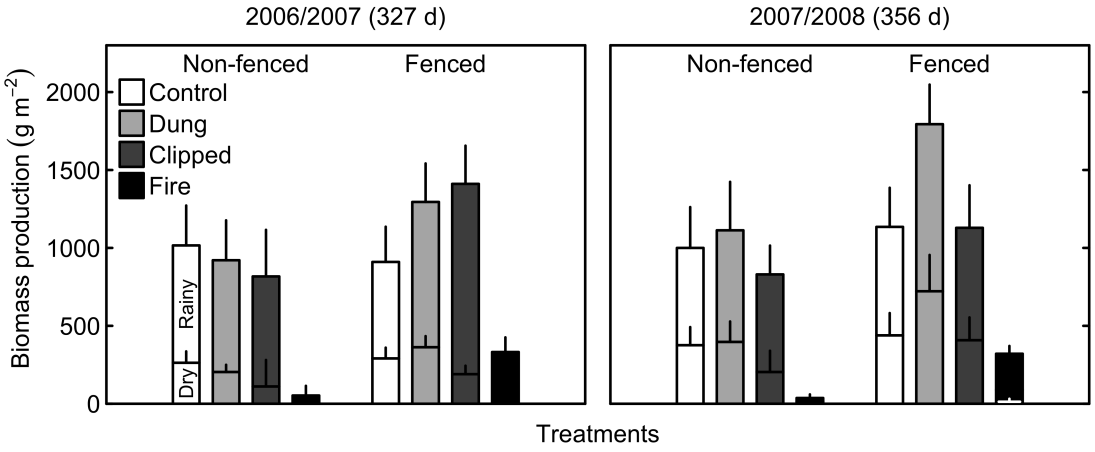

Figure 3.2: Biomass production (mean + 95% CI, n = 4 subplots, 6 plants per plot) for the first, drier year (May 2006 to April 2007; left panel), and for the second year with normal precipitation regime (May 2007 to April 2008; right panel). Biomass production is divided for the dry (bottom) and the rainy season (top).

Table 3.1: Above ground biomass production (g m^{-2}) of *F. orthophylla* over 4 studied periods in the Andean Altiplano (means, medians and 95% confidence intervals back transformed from $\log_{10}$).

		Dry season 2006			Rainy season 2006/2007			Annual
Treatment	Fence	Mean	Median	CI	Mean	Median	CI	production
Non-fenced	Control	263	271	206–336	753	819	561–1009	1016
Non-fenced	Dung	204	242	166–250	717	648	529–973	921
Non-fenced	Clipped	111	105	44–281	706	934	495–1005	817
Non-fenced	Fire	-	-	-	53	46	25–115	-
Fenced	Control	291	265	236–360	619	754	454–845	910
Fenced	Dung	363	343	304–434	932	1051	737–1179	1295
Fenced	Clipped	190	232	147–244	1221	1308	1017–1466	1411
Fenced	Fire	-	-	-	332	401	259–426	-

		Dry season 2007			Rainy season 2007/2008			Annual
Treatment	Fence	Mean	Median	CI	Mean	Median	CI	production
Non-fenced	Control	376	370	287–492	624	695	440–886	1000
Non-fenced	Dung	397	452	299–528	716	971	500–1027	1113
Non-fenced	Clipped	204	304	122–340	626	643	483–811	830
Non-fenced	Fire	13	11	5–32	24	22	12–47	37
Fenced	Control	439	476	331–582	696	849	511–947	1135
Fenced	Dung	722	761	546–955	1072	1115	867–1326	1794
Fenced	Clipped	408	399	300–554	721	859	522–994	1129
Fenced	Fire	89	82	69–114	232	232	191–282	321

Table 3.2: Generalized linear model for the biomass production ($\log_{10}$) of *F. orthophylla* in 4 consecutive seasons in the Andean Altiplano.

Dry season 2006

Source	SS	df	MS	F	P
Fence	0.603	1	0.603	10.094	**0.002**
Fence/Treatment	1.512	4	0.378	6.335	**<0.001**
Error	7.043	118	0.060		

Rainy season 2006/2007

Source	SS	df	MS	F	P
Fence	2.311	1	2.311	26.553	**<0.001**
Fence/Treatment	13.127	6	2.188	25.142	**<0.001**
Error	13.836	159	0.087		

Dry season 2007

Source	SS	df	MS	F	P
Fence	4.400	1	4.400	40.065	**<0.001**
Fence/Treatment	23.504	6	3.917	35.670	**<0.001**
Error	16.803	153	0.110		

Rainy season 2007/2008

Source	SS	df	MS	F	P
Fence	3.563	1	3.563	34.768	**<0.001**
Fence/Treatment	19.059	6	3.176	31.001	**<0.001**
Error	15.677	153	0.102		

Table 3.3: Multivariate and univariate repeated measures generalized linear model for the biomass production ($\log_{10}$) of *F. orthophylla* along 4 consecutive seasons in the Andean Altiplano.

Multivariate

Between subjects

Source	SS	df	MS	F	P
Fence	1.722	1	1.722	14.374	**<0.001**
Fence/Treatment	2.139	4	0.535	4.462	**0.002**
Error	13.540	113	0.120		

Within subjects

Source	SS	df	MS	F	P
Season	14.960	3	4.987	61.926	**<0.001**
Season × Fence	0.165	3	0.055	0.685	0.562
Season × Fence/Treatment	2.046	12	0.170	2.117	**0.016**
Error	27.299	339	0.081		

Univariate

Test for Fence

Source	SS	df	MS	F	P
Dry season 2006	0.535	1	0.535	8.879	**0.004**
Error	6.811	113	0.060		
Rainy season 2006/2007	0.369	1	0.369	3.646	**0.059**
Error	11.443	113	0.101		
Dry season 2007	0.852	1	0.852	9.406	**0.003**
Error	10.235	113	0.091		
Rainy season 2007/2008	0.131	1	0.131	1.203	0.275
Error	12.350	113	0.109		

Test for Fence/Treatment

Source	SS	df	MS	F	P
Dry season 2006	1.484	4	0.371	6.153	**<0.001**
Error	6.811	113	0.060		
Rainy season 2006/2007	1.053	4	0.263	2.600	**0.040**
Error	11.443	113	0.101		
Dry season 2007	1.010	4	0.252	2.786	**0.030**
Error	10.235	113	0.091		
Rainy season 2007/2008	0.638	4	0.159	1.459	0.219
Error	12.350	113	0.109		

Across the 4 studied periods, the season (or the 4 time points) explained more of the variation in the biomass production than the fencing or the additional treatment (always nested under fenced/non-fenced; Table 3.2). Tussock biomass production obviously was higher in wet (seasons 2 and 4) than in dry seasons (seasons 1 and 3). Fencing induced greater biomass production, but showed no significant interaction with season ($P = 0.562$), whereas additional treatments caused the variation in biomass production to become significant over time (significant interaction term $P = 0.016$).

Across all 4 seasons, fencing had an effect mainly during the dry seasons, marginally significant in the first rainy season and not statistically significant in the second rainy season (Table 3.2).

We calculated the biomass production using the constant land cover of 14.45% (non-fenced control) for all subplots except by fire (1.4% tussock land cover). Over all seasons, the constant land cover removed the fencing effect, but the overall treatment effect (nested under fence) was still significant. Not surprisingly, biomass production was still lower in the dry seasons (seasons 1 and 3) than in the rainy seasons (seasons 2 and 4) like in the previous analysis. However, fences did not stimulate biomass production ($P = 0.255$) when cover was assumed to be constant, and neither was there a significant interaction with season ($P = 0.562$), but the treatment effect over time was still variable (significant interaction $P = 0.016$). The fencing effect across the 4 seasons that was mainly significant during the dry seasons disappeared completely.

3.4.3 Ramet mortality, flowering and grazing

The number of ramets lost between two campaigns was higher in non-fenced then in fenced plots, however, the fencing effect on ramet loss was only detected in the first two seasons (data not shown). To standardize across these differences, we used fraction data to analyze the mortality, flowering and grazing impact.

Because new growth is tightly associated with leaf and ramet turnover, but would affect standing biomass crop if delayed, we analyzed the mortality responses to the various treatments (Table 3.4). In contrast to new ramet production, mortality was generally larger in the wet than in the dry season of both, the drier and the more humid year. Across all seasons, mortality was higher in non-fenced subplots in comparison to non-fenced ($P < 0.001$), and the treatments nested in fence had a significant effect on ramet mortality ($P < 0.001$). Fences decreased mortality during both dry seasons, but not during the rainy seasons. The highest mortality registered was for ramets in clipped non-fenced tussocks in the first dry season, followed by burnt tussocks, irrespective of the fencing condition. These high mortality rates may be associated with either a natural high turnover of short, new growing-ramets (in the case of burnt tussocks), or a difficult initial re-establishment of clipped and burnt tussocks.

Festuca orthophylla flowered during the rainy season only, and the intensity of flowering was more pronounced in the first rainy season. As expected, animal exclosure increased the fraction of flowering ramets per tussock across seasons ($P = 0.003$), and the treatments had an effect on flowering ($P < 0.001$). Dung addition increased flowering in the first rainy season in fenced conditions only, but clipping and fire treatments obviously reduced

Table 3.4: Percentage of ramet mortality, ramet grazing and ramet flowering measured in *F. orthophylla* (n = 1–5, mostly 4 marked ramets in n = 16 tussocks) over 4 studied periods in the Andean Altiplano.

Ramet Mortality

Fence	Treatment	Dry season 2006	Rainy season 2006/2007	Dry season 2007	Rainy season 2007/2008
Non-fenced	Control	7.7 ± 15.6	20.8 ± 23.2	10.8 ± 14.6	26.7 ± 28.8
Non-fenced	Dung	11.0 ± 19.7	29.6 ± 24.5	17.5 ± 18.7	22.5 ± 32.7
Non-fenced	Clipped	62.4 ± 29.8	35.2 ± 27.6	34.0 ± 27.0	44.3 ± 29.0
Non-fenced	Fire	-	39.4 ± 37.5	50.3 ± 30.1	49.0 ± 39.9
Fenced	Control	1.9 ± 6.4	19.2 ± 23.2	7.9 ± 10.5	27.4 ± 34.1
Fenced	Dung	1.7 ± 5.6	13.0 ± 15.7	7.8 ± 11.6	26.2 ± 26.4
Fenced	Clipped	15.0 ± 16.9	30.4 ± 22.3	12.3 ± 13.5	42.4 ± 32.4
Fenced	Fire	-	40.0 ± 31.2	40.1 ± 30.7	51.6 ± 29.1

Ramet Grazing

Fence	Treatment	Dry season 2006	Rainy season 2006/2007	Dry season 2007	Rainy season 2007/2008
Non-fenced	Control	6.3 ± 14.3	13.3 ± 23.3	6.4 ± 12.0	12.4 ± 20.8
Non-fenced	Dung	7.3 ± 14.2	7.1 ± 10.3	24.5 ± 22.4	6.7 ± 15.8
Non-fenced	Clipped	54.9 ± 32.3	10.4 ± 17.0	32.8 ± 23.4	28.1 ± 28.0
Non-fenced	Fire	-	46.2 ± 44.2	52.2 ± 36.4	40.8 ± 39.9

Ramet Flowering

Fence	Treatment	Dry season 2006	Rainy season 2006/2007	Dry season 2007	Rainy season 2007/2008
Non-fenced	Control	-	46.3 ± 28.1	-	19.7 ± 16.2
Non-fenced	Dung	-	42.5 ± 25.2	-	18.1 ± 21.9
Non-fenced	Clipped	-	1.9 ± 6.4	-	1.1 ± 5.2
Non-fenced	Fire	-	0.0 ± 0.0	-	0.0 ± 0.0
Fenced	Control	-	47.6 ± 24.8	-	36.4 ± 33.2
Fenced	Dung	-	60.4 ± 24.0	-	33.9 ± 29.0
Fenced	Clipped	-	16.3 ± 20.2	-	10.1 ± 23.8
Fenced	Fire	-	0.0 ± 0.0	-	0.0 ± 0.0

Table 3.5: Measured and corrected (for time bias) tussock land cover of *F. orthophylla* in the Andean Altiplano. Land cover was estimated by the line intercept method over aerial digital images in the 32 studied subplots.

Fence	Treatment	Land cover (measured; %)	Land cover (corrected; %)
Non-fenced	Control	12.9 ± 1.9	14.4 ± 1.1
Non-fenced	Dung	12.4 ± 2.1	13.9 ± 1.9
Non-fenced	Clipped	12.1 ± 3.3	13.6 ± 2.8
Non-fenced	Fire	0.5 ± 0.0	1.0 ± 1.0
Fenced	Control	16.4 ± 4.5	16.4 ± 4.5
Fenced	Dung	19.3 ± 3.4	19.3 ± 3.4
Fenced	Clipped	18.4 ± 1.5	18.4 ± 1.5
Fenced	Fire	3.3 ± 0.8	3.3 ± 0.8

inflorescence production (in the case of fire to zero), and the reduction in clipped tussocks was greater in non-fenced subplots.

In control tussocks the fraction of ramets with traces of grazing tended to be more abundant in the rainy season, but grazing pressure was higher during the dry season for all three treatments. Tussocks regrowing after fire had a general high grazing impact, followed by clipped tussocks. As for mortality, the largest grazing impact was for clipped tussocks in the first dry season (Table 3.4) probably due to the absence of the standing necromass removed during the clipping campaign.

3.4.4 Tussock land cover

Festuca-tussocks in the test area cover 14.4% ± 1.1 of the landscape (aerial photographs; n = 4, non-fenced control; mean ± sd, Table 3.5), and results numbers were quite similar for the *in situ* line intersept method (13.5% ± 6.1). Since our aerial pictures were not taken all in the same year, the land cover for pictures taken in the first year were corrected by adding the difference in the land cover for the same treatment (+1.5% cover between year 1 and 2, except in the fire treatment, where 0.5% cover was added).

The aerial photographs showed that fencing increased the land cover (Tables 3.5 and 3.6), and the treatments had a general significant effect on land cover as well. This overall treatment effect on cover was a net effect of none or positive effect in the fenced plots only. Our definition of cover does not apply to the fire and clipping treatments, and the cover data for plots having received llama dung do not differ significantly from controls (Table 3.7). However, fencing in combination with dung addition resulted in a marginally significant increase in the land cover after two years (non-fenced plus dung 13.9% ± 1.9, fenced plus dung 19.3% ± 3.4; Table 3.5). Thirty months after the single fire event, the mean cover was 1.0% for non-fenced areas, and 3.3% when burnt tussocks were protected by a fence.

Table 3.6: Generalized linear model for the corrected tussock land cover (arcsin transformed) of *F. orthophylla* in the Andean Altiplano.

Source	SS	df	MS	F	P
Fence	0.011	1	0.011	17.705	**<0.001**
Fence/Treatment	0.119	6	0.020	32.290	**<0.001**
Error	0.015	24	0.001		

Table 3.7: Tukey's HSD for the corrected tussock land cover (arcsin transformed) of *F. orthophylla* in the Andean Altiplano.

	F-Co	F-Du	F-Cl	F-Fi	nF-Co	nF-Du	nF-Cl	nF-Fi
F-Co	1.000							
F-Du	0.681	1.000						
F-Cl	0.933	0.999	1.000					
F-Fi	**<0.001**	**<0.001**	**<0.001**	1.000				
nF-Co	0.931	0.120	0.311	**<0.001**	1.000			
nF-Du	0.825	**0.069**	0.197	**<0.001**	1.000	1.000		
nF-Cl	0.794	**0.051**	0.152	**<0.001**	1.000	1.000	1.000	
nF-Fi	**<0.001**	**<0.001**	**<0.001**	0.885	**<0.001**	**<0.001**	**<0.001**	1.000

3.4.5 'Standing crop' biomass of Altiplano tussocks and new root growth

Based on the land cover presented here and above-ground biomass and necromass data based on individual tussocks (Chapter 2), we can now estimate above ground standing crop per unit land area for this semi-arid grassland. For biomass we arrived at 451 ± 161 g m^{-2} biomass and for necromass 546 ± 425 g m^{-2} per total land area, adding up to a phytomass of 996 ± 545 g m^{-2} (mean and sd for n = 9 non-fenced tussocks). Hence, biomass represents less than half of phytomass. These numbers illustrate that the annual above-ground biomass production of around 1000 g m^{-2} is nearly twice the above ground biomass, suggesting a mean biomass duration of half a year.

The root mass fraction was estimated as 21% (Chapter 2), which accumulates to 186 ± 125 g m^{-2} of total land area (n = 3 excavated tussocks). Adding rootstock biomass fractions (28%) brings the total pool size of roots and rootstock to 314 ± 178 g m^{-2} of total land area. The amount of roots harvested in the current coring campaign was significantly lower in fenced burnt subplots in comparison to control areas, but there was no difference between dunged and control. Based on the in-growth core, the root turnover per year data is 18.7% ± 5.3 (mean ± sd) for fenced, control areas (suggesting a *ca.* 5-year mean root duration). The new growth fraction in fenced subplots that received dung (21.1% ± 9.6) did not differ from fenced control, but burnt areas had less new root growth fraction (11.5% ± 14.5) than control. Converted to total land area, we estimate an amount of new root arrival of 35 ± 9 g m^{-2} a^{-1}. However, actual annual productivity is likely to be higher than what is seen in an emptied and refilled bore hole. The rate of root

stock biomass renewal/biomass turnover is unknown and hard to access, but if we assume a similar annual increment than in roots, the annual above- and below-ground biomass production arrives at close to 1100 g m^{-2} a^{-1}.

3.5 Discussion

This first ever year-round non-destructive assessment of tropical-alpine biomass production in a semi-arid climate arrived at mean annual rates larger than cool temperate high alpine grassland (range 170–470 g m^{-2}, Körner, 2003). However, scaling these temperate zone rates to a 12-month growing season (instead of the *ca.* 3 months) we arrive at 510–1410 g m^{-2} a^{-1}, similar to the annual production in the Andean Altiplano, despite the large differences in the land cover (14.4 *versus ca.* 70%). In a cool oceanic climate, such as in New Zealand, tall tussock productivity of 330–518 in a 7.5 month growing season (Williams, 1977, see introduction) would scale to 550–870 g m^{-2} if the growing season was extended to 12 months. The larger foliage production in *F. orthophylla* could be explained by the year-round high daytime temperatures and the high solar radiation in the Bolivian highlands.

It came as a surprise that fencing alone had only moderate effects on productivity at the given stocking rate and natural growth conditions (fenced *vs.* non-fenced controls). However, fencing had a general positive effect on foliage production (more pronounced during the dry periods), that was associated with a decrease in mortality during the dry periods, which may have resulted in the increase in tussock land cover in fenced areas. Hofstede and colleagues have reported that biomass was significantly reduced in Colombian Páramo grasslands under heavy grazing, but not under moderate grazing (Hofstede et al., 1995*b*). Grazing may in fact increase productivity, both due to compensatory growth in response to tissue removal and animal dung. Milchunas and Lauenroth (1993) examined productivity responses to grazing in 236 sites and found a stimulation in semi-arid low productivity grasslands only, supposedly due to the long evolutionary history of grazing. Yet, the stimulations compared to fenced areas were below 10%. Despite the long grazing history, the semi-arid tussock grasslands studied here presumably are more productive then the sites examined by Milchunas and Lauenroth (1993), and thus may be weakly responsive to moderate grazing. Burning is clearly not advisable as a treatment to improve pasture quality. Burnt tussocks recover very slowly as was shown elsewhere before. For instance, short stature buffalo grass (*Buchloe dactyloides*) recovered only 3 years after a natural fire event in Kansas (Launchbaugh, 1964). Recovery of tall tussocks may take even longer. In the Colombian Páramo, the grassland under low grazing pressure recovered the initial biomass only 7 years after the last fire event (Hofstede et al., 1995*b*). Similar to *Festuca orthophylla* burning tall snow tussocks in New Zealand (*Chionocloa rigida*) has disastrous consequences, and recovery was estimated to take 14 to 20 years in montane grassland (Gitay et al., 1992; Mark et al., 2000; Payton and Mark, 1979). In fact, at our site unfenced and burnt tussocks did not recover at all, because any new leaf growth was removed by camelids.

Ramsay reported a phytomass of 80–200 g m^{-2} for early-, late-, or early- and late-

clipped *Calamagrostis intermedia* in the Colombian Páramos, regrowing over 103–110 days, what represented 10-25% of the 794–837 g m^{-2} phytomass of an undisturbed area (Ramsay and Oxley, 2001). On the other hand, *Stipa tenuis* and *Poa napostaense* clipped in the beginning of the growing season achieved the same phytomass of undisturbed plants after a 7 months growing season in central, semi-arid Argentina (Becker et al., 1997). Regrowth of *F. orthophylla* in fenced and clipped areas tended initially to be reduced (first dry season after clipping), but was surprisingly increased by two fold in the subsequent rainy season, yielding 51% more foliage production over the first year, but returning to values similar to fenced control in the subsequent two seasons. Therefore, it is likely that *F. ortophylla* is recovering rapidly from sever defoliation while under animal exclusion, re-establishing the initial steady state in less than two years.

Growth and biomass production in natural grasslands including those at high elevation are well known to be nutrient-limited, and even small amounts of fertilizer addition can exert major effects on productivity (Bassin et al., 2007; Hiltbrunner and Körner, 2004; Körner, 2003). It is, thus, long-standing practice in many parts of the world to improve alpine pastures, at least in accessible areas, by manure addition. Surprisingly, enormous amounts of manure accumulating around overnight kraals in the Altiplano have not traditionally been allocated back to the rangeland. Our results show a positive overall effect of dung addition, particularly in the fenced areas during the first dry season. Surprisingly, no such effect was seen in non-fenced plots, although our assessment rests upon undamaged ramets. If sustainable, dung addition at the rate employed here would permit a 58% higher stocking rate with camelids as compared to unfertilized plots. The productivity effect of dung addition during the dry season, led to a higher foliage grazing reaching 24.5% in the second year as compared to 6.4% in unfertilized controls. Further, flowering was enhanced by dung addition during the first rainy season with 48% of flowering ramets in fenced control areas *vs.* 60% in fenced subplots that received dung.

With *ca.* 1 kg m^{-2} a^{-1}, the rates of biomass accumulation per total land area are quite high, much higher than one would expect in such a semi-arid rangeland. The most plausible explanation is that these tussocks are utilizing a far greater land area for water and nutrient acquisition than represented by their projected canopy area. Utilization of the space inbetween tussocks is, thus, a most likely mechanism explaining these high rates of productivity. The root sphere is covering an area *ca.* 6 times the size of the tussock projected area and, thus, has access to six times the precipitation per unit tussock area (corresponding to >1000 mm of precipitation). The degree of land cover has already been shown to be a most critical mechanism to cope with water shortage in such high elevation grasslands (Geyger, 1985). Given that tussock root spheres hardly overlap but rather leave unexplored inter-tussock space, there seems to be some leeway for increasing tussock density without losing the advantage of wide spacing in terms of water and nutrient relations, but also fire spreading. It remains to be explored how large the actual root-covered land area is. But based on our preliminary studies (Chapter 1), it seems tussock density could be enhanced by 30 to 50% before root spheres start to overlap. Current grazing pressure prevents tussock recruitment, so natural tussock mortality or man-made mortality by misuse of fire is currently not compensated by natural recruitment. Hence, in addition to llama dung distribution, grazing management with mobile fences seems

like an additional management option to retain higher camelid stocks without destructive consequences. From our unquantified observations, new tussock establishment occurs already in the first year after fencing. Hence, periodic camelid exclusion could assist in increasing tussock density and, thus, productivity per land area. There is no indication that low temperature per se has a major impact on productivity at these high elevations.

4.0 No compensatory growth of leaves in response to clipping in the tall tussock grass *Festuca orthophylla* in the Andean Altiplano

4.1 Abstract

Tall grass tussocks dominate the Andean highlands above 3800 m a.s.l., with often no other life form contributing significantly to standing crop biomass and productivity, thus, representing the dominant source of fodder for camelid grazing. To assess the productivity of these semi-arid tropical rangelands (350 mm of annual rainfall confined to a 4–5 months rainy season) is challenging to assess, given the 'evergreen' nature of leaves and the unknown periodicity of leaf growth. The aim of this study was to explore the seasonal course of new foliage formation, foliage duration, and the response of leaf elongation and emergence to simulated llama grazing (clipping). The census of *Festuca orthophylla* leaves in the Sajama National Park at 4250 m elevation (Bolivia) provided clear evidence that leaf production is not confined to the rainy season, but also occurs during the dry season. The mean leaf longevity is 141 days for peripheral control tillers (unclipped) and 169 days for central control tillers. No compensatory growth in response to clipping was observed. Leaves grow slower and reach shorter length during the dry season compared to the rainy season, and peripheral tillers are always shorter but more vigorous than central tillers (shorter intervals between the emergence of two leaves). Overall, this study suggests a *ca.* 2-fold replacement of foliage per year. The significant contribution of dry season leaf growth to annual production confirms earlier data from tiller demography and regrowth (after cutting) studies. We explain the continued growth in the dry season by, on average, six times greater soil area occupied by roots than by the leaf canopy, and thus, much greater water availability per tussock than meteorological data would suggest. Wide spacing of tussocks and a large root-sphere mitigate the impact of periodic drought on tissue formation, providing year-round forage for llamas.

4.2 Introduction

Herbivory has been a major, ecological impact, for as long as fossil records for vascular plants are available (Chaloner et al., 1991). The long interaction between plants and herbivores has selected for plants that can avoid or tolerate the removal of biomass, and on the other side, herbivores that can cope with plant's defences. Defoliation may have stimulat-

ing or retarding effects on plant growth. A compensatory stimulation of growth may result from a suite of effects, such as a reduction of self-shading, increase in nutrient availability, and an improvement of the water status of the remaining tissues. The ontogenetic decline in photosynthesis, a smaller fraction of senescent foliage, less new root growth, and a hormonal stimulation of apical meristems may further contribute to compensatory growth enhancement (Crawley, 1998; Dyer et al., 1993; McNaughton, 1983*a*,*b*). Yet, there is no consensus whether compensatory growth in response to defoliation is a general response as is often assumed (Belsky et al., 1993; Crawley, 1987). Different scales of measurements (spatial and temporal; Belsky, 1987; Belsky et al., 1993), and the different currencies (above-ground net production *versus* Darwinian fitness; cf. Crawley, 1998) may affect results. Additionally, the term of compensatory growth is used in a very broad sense, ranging from a partial substitution of the lost tissue, to an increase in biomass production (regrowth) in grazed compared to undisturbed vegetation. Responses may further differ depending on whether whole plants are treated (like in the case of mowing) or individual shoots or tillers are removed, with intact neighbour foliage.

According to the herbivore optimization hypothesis (Dyer et al., 1982), a moderate grazing level tends to increases the above-ground net primary production or fitness of grazing-tolerant plants. Nevertheless, the literature that evidences a consistent increase of biomass production due to grazing is meagre (Crawley, 1987; Westoby, 1989). Milchunas et al. (1988) developed a model to predict the effects of grazing by large herbivores in grasslands, based on gradients of moisture availability *versus* evolutionary history of grazing. The model was later validated by a meta-analysis based on a worldwide, 236-site data set, compiled from studies evaluating the impact of grazing on vegetation (Milchunas and Lauenroth, 1993). Semi-arid grasslands with a long evolutionary history of grazing, low primary production and low to moderate grazing pressure appeared as the most likely situation in which compensatory increases in biomass production might occur.

Over the whole Andean Altiplano, the husbandry of camelids is still practiced in the traditional way, where animals graze unfenced during the day, and are gathered at night. Llamas and alpacas have been selected from wild camelids since ancient time, with livestock peak in the XI and XII centuries during the Inca Empire (Cardozo, 2007). The natural Altiplano pasture consists of the tall tussocks of *Festuca orthophylla*, the dominant species in the dry pajonales, that covers vast rangeland areas between 3600 and 4680 m a.s.l. (Chapter 2). Shrub species from the genera *Baccharis* and *Parastrephia* are far less frequent, and small annual and perennial herbs emerge only during the rainy season of the austral summer. This intra-tussock vegetation plays an important role in the nutrition due to high nitrogen content (Patty et al., 2010). Nevertheless, *Festuca orthophylla* is the principal component of the ecosystem's primary production and has major importance for the livestock's diet. A management of the pastures is almost inexistent, with the exception of burning of old tussock individuals. However, the benefits of fire are controversial, as the post-fire regrowth is severely affected by grazing, and rather slow even under animal exclusion (Chapter 3).

The long plant-animal interaction may have led to adaptations of *Festuca* tussocks to regular grazing, and compensatory growth could be one of the adaptive responses, together with the semi-arid climate of the Altiplano, and the low primary production of *F.*

orthophylla (Chapter 3), conditions that seem to match those where compensatory growth is expected (Milchunas and Lauenroth, 1993). Hence, we hypothesized that clipping (simulation of grazing) accelerate growth in *Festuca orthophylla*. Accordingly, we asked the specific questions: (1) does clipping of the fully-expanded leaves accelerate the growth of the next leaf on the same tiller, (2) does clipping stimulate elongate the life of the next generation of leaves, or (3) enhance the rate of leaf emergence? In addition, we tested if clipping causes different responses in the above-mentioned parameters for tillers in the centre and in the periphery of the tussocks.

4.3 Material and methods

4.3.1 Study area

In the western part of the Bolivian Altiplano, close to the Chilean border, high mountain wildlife has been protected along an elevational range of 4200–6542 m a.s.l. since 1939 by the Sajama National Park (S 18° 08' W 68° 58'). In spite of its protected status, more than 5000 indigenous inhabitants (census of 2002) are allowed to continue the traditional camelid husbandry (llamas and alpacas) in the lower parts of the park. The humid depressions represent the so-called 'bofedales', with full cover of short-stature vegetation. The more abundant, slightly elevated terrain is well drained, and dominated by *Festuca orthophylla* ('pajonales') a tall, widely spaced tussock grass (land cover = 14.4%).

This semi-arid region is characterized by year-round low temperatures: average of daily means is 2.3° C for 'winter' and 10.7° C for 'summer' (rainfall season). Temperature seasonality is low, but the diurnal amplitude is very high (8.6% of the days showed an amplitude in air temperature of more than 30 K between 2003–2008; Chapter 2). The annual precipitation is 300–350 mm (Hardy et al., 1998), and is concentrated between November and March, with strongest rainfall in January and February. The dry, cloudless winter without snow cover increases evaporative demand, accentuating the aridity of the region.

4.3.2 Plant material and measurements

For this study, initiated on February 13^{th} 2008, we used fenced test plots that have been excluding animals since April 2006 (Chapter 2). In each of the four fenced, control subplots we selected 4 representative tussocks (mean diameter 43 ± 7 cm, height 58 ± 12; mean ± sd) to observe the seasonal leaf expansion and the response of individual tillers to defoliation (Fig. 4.1). In each plant we marked eight tillers with a recent, just emerging leaf, using coloured plastic beads: four tillers close to the centre of the tussock, any other four at the periphery. To simulate grazing, half of the tillers were clipped, *i.e.* all fully-expanded leaf-blades were cut at 3 cm distance of the leaf's ear, but the youngest expanding leaf-blade (<3 cm visible) in each tiller was left intact. We measured the length of this newly expanding leaf (L1), using the ear of the second youngest, fully-expanded leaf as a reference. Marked tillers were revisited periodically (5 to 20-day intervals over a period of 188 consecutive days) to measure the length of the youngest leaf, and note its

Figure 4.1: Average size tussocks of *Festuca orthohylla* in the Sajama National Park (4250 m a.s.l.) in the Bolivian Altiplano.

phenological state (green, senescent or dead). The same traits were recorded for a second cohort of emerging leaves (L2) later in the year.

For this experiment we used 8 marked tillers in each of 16 tussocks. Of these 8 tillers, each of 2 tillers had the same combination of treatment × position (so the replicate were the tussocks, *i.e.* n = 16), and the value used for statistics was the average of these two tillers with the same combination of treatment × position per tussock. Leaves that died suddenly during the expansion were excluded from the analysis.

4.3.3 Statistics

We used a best fit (coefficients a and b) exponential function to obtain the growth curve for each individual leaf studied ($Leaf\ length\ =\ maximum\ length + a \times exp(-exp(b) \times day)$. With these curves we regressed the date of leaf emergence (length = 0) of the first and second leaf cohort census. For a graphical illustration we averaged the parameters a and b for the individual leaves. For each leaf, we calculated the slope of the initial growth rate

and the final leaf length (leaf blade only). We also calculated the interval between the emergence of the first and second cohort. The onset of leaf senescence and leaf longevity were measured in the first leaf cohort only. At the end of the experiment (188 days) we had a mortality of 60% of all leaves present initially. Since surviving leaves of the first cohort examined often maintained 1–3 cm of green tissue at the base of the leaf blade for a long time, we considered all leaves dead that reached this state.

We followed the protocol of Zuur et al. (2009) to check the distribution of residuals and corrected for the heterogeneity of residuals between fixed factors when necessary. All parameters were analysed with fixed-effect models, and the fixed factors were tiller position (centre *versus* periphery) and treatment (control *versus* clipped). The only parameter for which a transformation was needed was the final leaf length for the second cohort, and the transformation used was $\log_{10}$. All statistics and graphics were done with R 2.10.0 (R Development Core Team, 2009).

4.4 Results

For the first leaf cohort, initial leaf elongation rate in clipped tillers was not different from control tillers ($P = 0.404$, Tables 4.1 and 4.2), but the initial leaf growth rate was higher for central tillers ($P < 0.001$), than for peripheral tillers. For the second cohort of leaves, which emerged during the dry season, there was neither a clipping ($P = 0.716$) nor a position effect ($P = 0.292$). However, there was a significant interaction between these two factors: clipping decreased the initial expansion rate in the centre of the tussock, but increased the leaf expansion rate in the periphery.

Clipping had only a marginally negative effect on the final length of leaves, both in the first cohort emerging at the peak of the rainy season ($P = 0.081$), and in the second cohort of leaves, emerging during the dry season ($P = 0.072$). However, mature leaves from central tillers were longer for both leaf cohorts ($P < 0.001$).

After clipping, the onset of leaf senescence in the following leaves on the same tiller was delayed ($P = 0.020$). The position of the tiller had no effect on the start of leaf senescence in leaves (first cohort data only, $P = 0.121$). Clipping had no effect on leaf longevity ($P = 0.364$), but leaves from central tillers always lived longer than leaves from peripheral tillers ($P < 0.001$). Finally, the interval between the emergence of the first and the second leaf cohort did not show a clipping effect ($P = 0.404$), but the emergence of the second cohort was earlier (shorter interval) in peripheral tillers compared to central tillers ($P < 0.001$). Overall, there were no clipping effect on leaf dynamics of tillers of *F. orthophylla*, but leaf turnover was more rapid in the periphery of the tussock (shorter longevity and shorter interval between two leaf cohorts; Fig. 4.2).

4.5 Discussion

The results of this assessment of leaf dynamics in tall Altiplano tussock grasses revealed a 4.7 to 5.6 months leaf duration and a surprising continuation of leaf expansion and emergence during the long dry season. With a given standing crop of foliage, this means

Table 4.1: Dynamic and traits of leaves of *Festuca orthophylla* from non-clipped (control) or clipped tillers in central or peripheral position (mean ± sd; original n = 16 tussocks [a]). L1 and L2 refer to the first (rainy season) and the second (beginning of dry season) leaf cohort after the beginning of the experiment

Response variable	Centre		Periphery	
	Control	Clipped	Control	Clipped
Leaf elongation rate (mm d^{-1}; L1)	3.8 ± 0.9 (16)	3.6 ± 1.0 (16)	2.7 ± 1.0 (15)	2.3 ± 0.7 (14)
Leaf elongation rate (mm d^{-1}; L2)	3.0 ± 0.9 (16)	2.7 ± 1.0 (14)	2.7 ± 0.8 (14)	3.3 ± 1.1 (13)
Final leaf length (cm: L1)	17.0 ± 3.0 (16)	16.3 ± 4.2 (16)	10.6 ± 3.0 (15)	10.3 ± 3.3 (14)
Final leaf length (cm; L2)	11.3 ± 3.1 (16)	9.8 ± 2.0 (10)	8.4 ± 1.4 (14)	8.1 ± 1.7 (13)
Beginning of senescence (d; L1) [b]	96 ± 17 (16)	105 ± 16 (16)	90 ± 24 (15)	101 ± 18 (14)
Longevity (d; L1)	169 ± 31 (16)	175 ± 20 (16)	141 ± 42 (15)	149 ± 30 (14)
Time to leaf emergence (d ;L2) [b]	54 ± 15 (16)	52 ± 16 (10)	40 ± 12 (14)	38 ± 8 (13)

[a] Leaves that died during elongation, or leaves that were too young to calculate all parameters were not used.
[b] Measured as leaf age in days, and not days of the year.

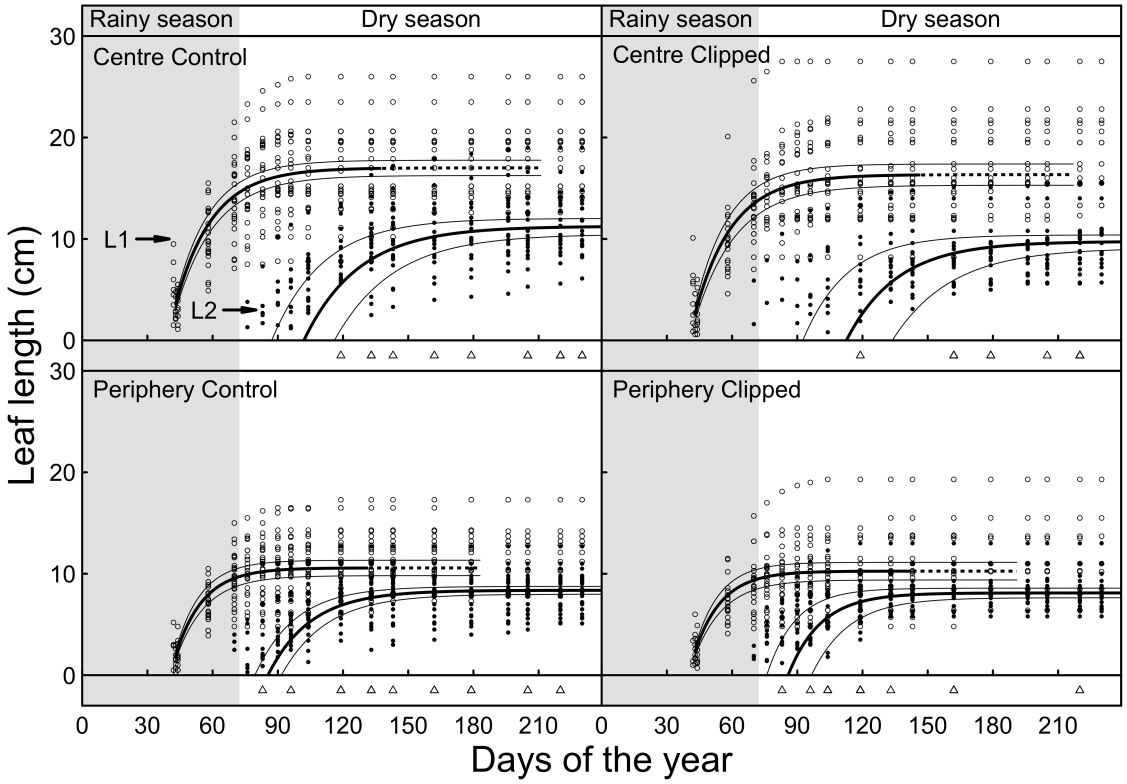

Figure 4.2: Analysis of variance for final leaf length and leaf elongation rate of two cohorts of leaves (L1 and L2) in control or clipped tillers, at central or peripheral position in the *Festuca orthophylla* tussock (n = 13–16 tussocks).

Table 4.2: Effect of clipping (clipped *versus* control), tiller position position (centre *versus* periphery), and season (rainy versus dry) on the final leaf length, leaf growth rate, beginning of senescence, longevity and time to leaf emergence in tillers of *Festuca orthophylla* (mixed effect model)

Response variable	Factor	DF	F-value	P-value
Initial leaf elongation rate (L1)	Clipping	1	0.71	0.404
	Position	1	26.67	< **0.001**
	Clipping × Position	1	0.18	0.671
Initial leaf elongation rate (L2)	Clipping	1	0.13	0.716
	Position	1	1.14	0.292
	Clipping × Position	1	7.19	**0.011**
Final leaf length (L1)	Clipping	1	3.21	**0.081**
	Position	1	63.00	< **0.001**
	Clipping × Position	1	0.06	0.813
Final leaf length (L2; $\log_{10}$)	Clipping	1	3.43	**0.072**
	Position	1	25.17	< **0.001**
	Clipping × Position	1	1.32	0.259
Beginning of senescence (L1)	Clipping	1	5.90	**0.020**
	Position	1	2.51	0.121
	Clipping × Position	1	0.13	0.713
Leaf longevity (L1)	Clipping	1	0.84	0.278
	Position	1	14.98	< **0.001**
	Clipping × Position	1	0.16	0.902
Time to leaf emergence (L2)	Clipping	1	0.71	0.404
	Position	1	16.53	< **0.001**
	Clipping × Position	1	0.00	0.996

that annual leaf productivity should be roughly twice leaf biomass, provided no other tiller stages are included than the ones assessed here. Clipping hardly affected leaf dynamics (no compensatory growth), and there is a clear distinction in vigour between peripheral and central tillers, the latter ones being larger, but 'slower' than the first. It follows from the tussock's architecture (Fig. 4.1) that central tillers are longer and also have longer leaf blades than peripheral tillers, and therefore it is not possible to separate the effect of position from the effect of the length of the tiller as such, but we consider the confounding of size and position of tillers intrinsic to the way these tussocks are shaped.

Initial leaf expansion rate in *F. orthophylla* rather seemed to be determined by tiller position in the tussock during the rainy season, with leaves of more central tillers expanding faster than leaves of peripheral tillers. However, for the leaf cohort emerging in the beginning of the dry season, the interaction between position and clipping points at accelerated initial expansion of peripheral leaves and slowed initial elongation of leaves in the centre of the tussocks. Further, we observed a rather linear rate of leaf elongation that stopped quite abruptly when leaves reached their maximum size in the leaf first (wet season) cohort, contrasting the findings for *Calamagrostis effusa* (Hofstede et al., 1995*a*), in which expansion rate decreased gradually with increasing leaf length.

As discussed in the introduction, compensatory growth in response to either artificial (clipping) or natural foliage removal (grazing, browsing) is not a universal response. Similar to the results of our study, re-growth of young leaves of individual ramets containing several tillers showed no effect of clipping in *Nardus stricta* along a clipping gradient (0–3 inter-connected neighbour tillers clipped, Grant et al., 1996). On the other hand, narrow-leaved tall tussocks of *Chionochloa rigida* (in New Zealand, similar in size and stature to *F. orthophylla*) showed a 21% growth stimulation (new leaf elongation) after almost complete removal of leaf blades (Rowley, 1970). In contrast, Hofstede et al. (1995*a*) found a reduction of initial leaf expansion rate with increasing grazing intensity in *Calamagrostis effusa* tussocks in the Colombian Páramos.

Clipping had only a marginally significant effect on the final length of the two generations of leaves studied, in both cases leaves growing in clipped tillers tended to be shorter. Shorter leaves in response to clipping were also reported for potted *Poa liguralis* of the Patagonian arid steppe and in grazed *Kobresia myosuroides* in an alpine meadow in Yucon, Canada (respectively, McIntire and Hik, 2002; Rotundo and Aguiar, 2008). However, both *Poa liguralis* and *Kobresia myosuroides* compensated for the shorter leaves, by producing more leaves per tiller. Accordingly, increasing clipping intensity in *Leymus chinensis* resulted in decreasing shoot final length, and tillering decreased only in 100%-clipped individuals in one of two studied years, and resulted in a general lower biomass accumulation in clipped plants (Liu et al., 2012).

The rate of new leaf emergence was not enhanced in clipped *F. orthophylla tillers*, but we cannot exclude a faster rate of tillering (not studied here). In the more peripheral tillers, leaf emergence generally occurred earlier than in more central tillers, irrespective of clipping treatment, which may compensate for their somewhat shorter size compared to more central tillers. In *Festuca orthophylla*, the only trait of leaf dynamics that responded to clipping in a compensatory way was the beginning of senescence, with leaves of clipped tillers delaying senescence, although final leaf duration was not affected.

The responses of *Festuca orthophylla* to drought clearly contrast other reports of a cessation of leaf elongation during the dry season for tussocks living in arid environments (Busso and Richards, 1993, 1995; Pugnaire et al., 1996). Although initial leaf elongation rates tended to be slower in *F. orthophylla* during drought, leaf blade elongation and leaf emergence were never completely suspended till late in the dry season (emergence of a third leaf cohort was observed; Fig. 4.2). The sustained growth of *F. orthophylla* during the long rainless season may reflect adequate water availability as was already implied by the transpiration studies (Geyger, 1985). A likely mechanism is the wide root sphere of the grass tussocks expanding into bare land in a landscape with low land cover (Chapter 1), causing biomass production to be larger than expected from rainfall data. Further, the prioritizing of peripheral tillers (higher leafing and lower effect of drought in initial rate of leaf elongation) over central tillers may result from a larger intra-tussock competition or clonal age (old centre, young periphery). In *Eragrostis curvula*, the removal of either live leaves or dead plant material stimulated tiller recruitment in the centre of the tussock compared to undisturbed tussocks, indicating that the tussock centre is a highly competitive environment, with both space constraints (crowding) and light extinction as important drivers (Ursino, 2009).

Leaf longevities of about half a year are quite common in perennial alpine plants in a tropical environment. Diemer (1998) reported 193 ± 19 days for several species in the Ecuadorian Paramos at *ca.* 4000 m elevation with much shorter duration of only 41 to 95 days (68 ± 4 days) in 29 herbaceous perennials in 2600 m a.s.l. in the Alps (Diemer et al., 1992). In the current study we assessed leaf longevity during the rainy and early dry season. Drought may enhance longevity as was shown for semi-arid regions (Casper et al., 2001; Sandquist and Ehleringer, 1998). Even in a temperate climate deciduous tree-species in Central Europe maintained leaves longer than usual during an exceptionally warm and dry summer (Leuzinger et al., 2005), however, even more severe drought would lead into drought deciduousness, as is well known from seasonal tropical forests. Assuming that the dry season (not explored here) leads to prolonged leaf duration in *F. orthophylla*, the average longevity across the year would be larger than reported here. Finally, since the total green leaf biomass of these tussocks is *ca.* 170 g d.m. m^{-2} of land area (unpublished data set from Chapter 1), a leaf turnover of half a year would yield a total green leaf production of 340 g m^{-2} land area a^{-1}. This estimate does not account for the production of leaf sheets, tillering and flowering, hence may be seen as a conservative, low-end estimate of the forage productivity of this landscape.

In conclusion, we observed no compensatory growth in *Festuca orthophylla* in response to partial foliage removal as occurs during camelid grazing. Nevertheless, we believe that clipping was 'sensed' by tillers, since it delayed the onset but accelerated the progression of leaf senescence, so, overall longevity was not affected. Continuation of leafing and leaf elongation during the long dry season is in line with ramet dynamics and regrowth after almost complete canopy removal (Chapter 3) and underlines the extremely efficient ways of moisture and space utilization in these tussocks. Wide spacing permits greater moisture availability per tussock and, thus, permits year-round production of new foliage (fodder) in this semi-arid high altitude ecosystem.

5.0 Summary

Tropical and subtropical high elevation grasslands are generally dominated by tall tussock grasses, a life form that seems to dominate in year round cold climates but otherwise quite different soil moisture regimes, from very wet (New Guinea, New Zealand, Ecuador) to rather dry, even semi-arid, as is the case in the NW-Argentinan and Bolivian Altiplano. The biomass production of these vast areas is largely unknown, since the classical harvesting technique cannot be applied in perennial vegetation without affecting growth. Given the steady increase in land use intensity, such information is needed to estimate the carrying capacity of these vast rangelands. In this thesis, I developed the needed non-destructive tools and applied them for a 30-month productivity analysis in the Bolivian Altiplano. The work was conducted in Sajama National Park at 4250 m elevation. The monthly mean temperature in the study area varies between 10.7 (December) and 2.3 (July), and annual precipitation averages at *ca.* 350 mm, most of this falling as rain between December and March (the austral summer). The study plant, *Festuca orthophylla*, is a tall (up to 1 m, mostly around 60 cm) tussock forming grass that represents more than 90% of all biomass in many parts of the Altiplano, including the study area. Forming clones of initially compact, but later fragmented shape, persisting many decades, this species is characteristic for the appearance of the semi-arid, Andean landscape over thousands of square kilometers at elevations between 3600 and 4600 m a.s.l. As a first step, I analysed the clonal structure, the morphology and biomass allocation in representative tussocks (Chapter 2). The core of the theses is related to the tussock biomass production using a demographic approach and land cover data (Chapter 3), followed by an assessment of seasonal leaf dynamics (Chapter 4).

Plant growth is driven by the rate of photosynthetic uptake of carbon, the loss of carbon and by allocation of photoassimilates to certain plant compartments, which leads to particular morphologies. Plant performance, vitality and persistence of a plant are affected by this partitioning process and vice versa. Under harsh climatic conditions such as cold temperature and seasonal drought, perennial plants invest more in below-ground than above-ground structures. As shown in Chapter 2, *Festuca orthophylla* does not match to this 'rule'. The shallow rooting system represents only 21% of total biomass. The tussock base (root-stocks, tiller meristems and the network of branching below-ground shoots), comprises 28% of the total biomass. Although partly below the soil surface, much of this biomass compartment is functionally above-ground (belonging to shoots). With their below-ground position, tiller meristems are protected against grazing and trampling by camelids as well as against fire and freezing. Fifty one percent of the biomass is

above-ground (live leaves and inflorescences). In terms of phytomass (including attached necromass), 75% is above-ground. On average, a tussock consists of 3200 tightly packed tillers (56% are live). Tillers emerge predominantly intravaginally (*i.e.* within the leaf sheath of an existing mother tiller), resulting in dense canopies with strong self-shading: eighty percent of green foliage experience less than 50% of the incident light. The most important Altiplano plant species thus, exerts morphological traits in favour of protection and survival rather than productivity.

As mentioned above, primary production cannot be measured by repeated harvesting in conditions of continuous growth without interfering with growth. With a non-destructive method, based on the number of leaves produced per ramet per time, length to weight ratios of leaves, ramet density within tussocks, birth, growth and death of leaves in ramets and land cover by tussocks, we estimated the primary production per total land area. *Festuca orthophylla* yielded an annual biomass production of *ca.* 1 kg m^{-2} in both, a relatively dry and a normal year, hence the difference in precipitation (327 mm *vs.* 384 mm) had no effect. Surprisingly, fencing alone had only moderate effects on productivity at the given stocking rate and natural growth conditions. The addition of dung in fenced areas increased the biomass production in comparison to unfenced areas where dung has been distributed. Within fenced subplots, clipping reduced the biomass production in the first dry season, but increased the biomass production in the subsequent rainy season. Biomass production after fire was near to zero, and fire was the treatment which had the greatest benefit of fencing. New leaves emerged throughout the year, hence, there was no period of complete inactivity despite the 7–8 months rainless period. Ramet mortality (associated with ramet turnover and, thus, new ramet production) was higher during the rainy season, and fencing reduced mortality during the dry season, but not during the rainy season. Fencing also had no effect on flowering, but clipping and fire suppressed flowering. New root arrival in in-growth cores made up *ca.* 19% $\pm$ 5 of the original root biomass in bore hole. Llama dung addition had no effect on new root arrival, but fire decreased relative root production in in-growth cores. The lateral roots of *Festuca orthophylla* tussocks growing into the large inter-tussock area compensate for the low rates of precipitation (roots spheres are 6 times larger than tussock canopy area. Continuous new leaf production despite strong moisture seasonality explains year-round grazing by camelids in this semi-arid high mountain ecosystem.

A 188 days census of *Festuca orthophylla* leaves provided clear evidence for leaf production in both the rainy and the dry season, a mean leaf duration of 141 days for peripheral tillers and 169 days for central tillers, and no compensatory growth response. Leaves grow slower and reach shorter length during the dry season compared to the rainy season, and peripheral tillers are shorter but more vigorous than central tillers (lower drought effect). Overall, this study suggests a nearly 2-fold replacement of foliage per year. The significant contribution of dry season leaf growth to annual production confirms earlier data from ramet demography and regrowth (after cutting) studies, and is most likely related to the 6 times greater soil occupancy by roots than by the leaf canopy. Wide spacing of tussocks and a large root sphere mitigate the impact of periodic drought on tissue formation providing year-round forage for llamas.

In conclusion, our data provide a quantitative characterisation of the architecture and

dry matter investment of this dominant Altiplano species, the first year-round productivity estimation for a high-elevation tropical, grassland, and a detailed assessment of leaf dynamics for the rainy and the dry season. In a number of ways the traits exhibited, contrast *Festuca orthophylla* from other, non-woody, high elevation taxa. In particular, the foliage of these tussocks operates at temperature close to that of the free atmosphere, while at the same time, providing shelter to below-ground shoot meristems. The large amount of dead plant material constrains photosynthetic light interception, and reflects slow rates of decomposition, a likely trade-off of generally poor nutrional quality (Patty et al., 2010), which, in turn, relates to the heavy herbivory pressure. The rates of biomass accumulation per unit of tussock area are quite high, much higher than one would expect in such a semi-arid rangeland. The most plausible explanation is that these tussocks are utilizing a far greater land area for water and nutrient acquisition than represented by their projected canopy area. The space in-between tussocks is, thus, a most likely mechanism explaining these high rates of productivity. The degree of land cover has already been shown to be a most critical mechanism to cope with water shortage in such high elevation grasslands (Geyger, 1985). Given that tussock root spheres do not overlap but rather leave unexplored inter-tussock space, there seems some leeway for increasing tussock density without losing the advantage of wide spacing in terms of water and nutrient relations. It remains to be explored how large the actual root-covered land area is. It seems tussock density could be enhanced by 30 to 50% before root spheres start to overlap. Current grazing pressure prevents tussock recruitment, so natural tussock mortality or man-made mortality by misuse of fire is currently not compensated by natural recruitment. Hence, in addition to llama dung distribution, grazing management with mobile fences seems like an additional management option to retain higher camelid stocks without destructive consequences, From our unquantified observations new tussock establishment occurs already in the first year of fencing. Thus, periodic camelid exclusion could assist in increasing tussock density and, thus, productivity per land area. There is no indication that low temperature *per se* has a major impact on productivity at these high elevations. We observed no compensatory growth in *Festuca orthophylla* in response to foliage removal. Nevertheless, we believe that clipping was a stimulus sensed by the tillers since it delayed the onset of leaf senescence, although not overall longevity. Continuation of leaf elongation during the long dry season is in line with a previous analysis of ramet dynamics and re-growth and underpins the extremely efficient ways of moisture and space utilization in these tussocks. Wide spacing permits greater moisture availability per tussock and, thus, permits year-round production of new foliage (fodder) in this semi-arid high altitude ecosystem.

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6.0 Supplementary material

Figure 6.1: Telescope antenna used to take aerial pictures of the studied area.

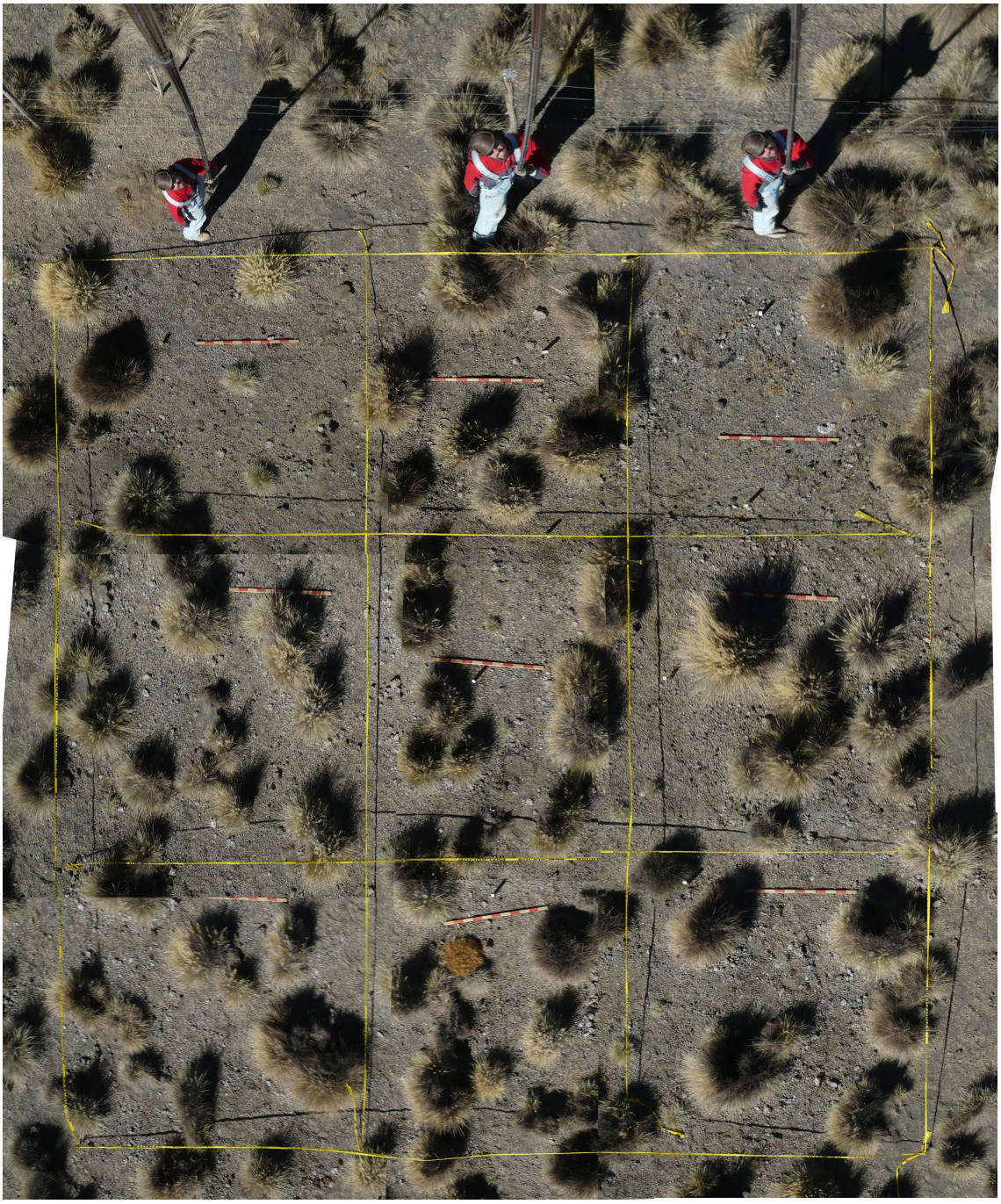

Figure 6.2: Example of aerial picture of a studied area.

Table 6.1: Tukey's HSD for the biomass production ($\log_{10}$) of *F. orthophylla* in 4 consecutive seasons in the Andean Altiplano.

Dry season 2006

	F-Co	F-Du	F-Cl	nF-Co	nF-Du	nF-Cl
F-Co	1.000					
F-Du	0.747	1.000				
F-Cl	**0.096**	**0.001**	1.000			
nF-Co	0.990	0.357	0.336	1.000		
nF-Du	0.249	**0.007**	0.998	0.617	1.000	
nF-Cl	**0.024**	**0.002**	0.502	**0.059**	0.355	1.000

Rainy season 2006/2007

	F-Co	F-Du	F-Cl	F-Fi	nF-Co	nF-Du	nF-Cl	nF-Fi
F-Co	1.000							
F-Du	0.440	1.000						
F-Cl	**0.013**	0.875	1.000					
F-Fi	**0.074**	**<0.001**	**<0.001**	1.000				
nF-Co	0.976	0.961	0.210	**0.004**	1.000			
nF-Du	0.995	0.891	0.119	**0.008**	1.000	1.000		
nF-Cl	0.897	0.996	0.405	**0.001**	1.000	0.999	1.000	
nF-Fi	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	1.000

Dry season 2007

	F-Co	F-Du	F-Cl	F-Fi	nF-Co	nF-Du	nF-Cl	nF-Fi
F-Co	1.000							
F-Du	0.318	1.000						
F-Cl	1.000	0.158	1.000					
F-Fi	**<0.001**	**<0.001**	**<0.001**	1.000				
nF-Co	0.997	**0.060**	1.000	**<0.001**	1.000			
nF-Du	1.000	0.127	1.000	**<0.001**	1.000	1.000		
nF-Cl	0.158	**<0.001**	0.304	**0.004**	0.526	0.383	1.000	
nF-Fi	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	1.000

Rainy season 2007/2008

	F-Co	F-Du	F-Cl	F-Fi	nF-Co	nF-Du	nF-Cl	nF-Fi
F-Co	1.000							
F-Du	0.474	1.000						
F-Cl	1.000	0.602	1.000					
F-Fi	**<0.001**	**<0.001**	**<0.001**	1.000				
nF-Co	1.000	0.178	0.998	**0.001**	1.000			
nF-Du	1.000	0.567	1.000	**<0.001**	0.998	1.000		
nF-Cl	1.000	0.206	0.998	**0.001**	1.000	0.999	1.000	
nF-Fi	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	1.000

Curriculum Vitae

José Alberto Fernandez Monteiro
Nationality: Brazilian and Spanish
Born on 1st December 1980; single.

Bläsiring 15
CH-4057 Basel
+41 (0)76 529 80 50
fernandez.monteiro@gmail.com

Professional Experience

May 2011–Apr 2012 Managing Editor of the open-access, scientific journal *Sustainability* (http://www.mdpi.com/journal/sustainability) at MDPI AG.
MDPI (http://www.mdpi.com) is currently the 3rd biggest open access publishing house in number of papers published per year. In this position I was in charge of coordinating and controlling the peer-review process, attracting authors to the journal and developing and setting up special issues on hot topics.

Aug–Oct 2010 Field assistant in the project TREELIM (http://pages.unibas.ch/botschoen/treelim/index.shtml).

Aug–Dez 2002 Assistant of Plant Physiology I in the course of Biological Sciences at UFSCar.

Feb–Jun 2002 Assistant of Embryology in the course of Biological Sciences at UFSCar.

Education

2006–2010 **PhD in Botany**, University of Basel, Switzerland, with emphasis in Ecology, supported by the Swiss Agency for Development and Cooperation (SDC) and the Swiss National Science Foundation (SNF).
Thesis: "Functional morphology and productivity of a tussock grassland in the Bolivian Altiplano", supervised by Erika Hiltbrunner and Christian Körner.

2004–2006 **Master of Science in Ecology**, University of Basel, Switzerland, supported with scholarship of the Federal Commission for Scholarships for Foreign Students (FCS).
Thesis: "Epiphytes in a CO_2 enriched world", supervised by Gerhard Zotz and Christian Körner.

1998–2002 **Bachelor of Sciences in Biology**, Federal University of São Carlos (UFSCar), Brazil.
Thesis: "Apparent carboxylation efficiency and relative stomatal and mesophyll limitations of photosynthesis in an evergreen cerrado species during water stress", supervised by Carlos H.B.A. Prado.

1986–1997 Colégio Visconde de Porto Seguro, German School, Valinhos, Brazil.

Publications

2011 Monteiro J.A.F., Hiltbrunner E., Körner C., Functional morphology and microclimate of *Festuca orthophylla*, the dominant tall tussock grass in the Andean Altiplano. *Flora* 206:387–396.

2010 Portes M.T., Damineli D.S.C., Ribeiro R.V., Monteiro J.A.F., Souza G.M., Evidence of higher photosynthetic plasticity in the early successional *Guazuma ulmifolia* Lam. compared to the late successional *Hymenaea courbaril* L. grown in contrasting light environments. *Brazilian Journal of Biology* 70(1):75–83.

2009	Monteiro J.A.F., Zotz G., Körner C., Tropical epiphytes in a CO_2-rich atmosphere. *Acta Oecologica* 35:60–68.
2006	Monteiro J.A.F., Prado C.H.B.A., Apparent carboxilation efficiency and relative stomatal and mesophyll limitations of photosynthesis in an evergreen species during water stress. *Photosynthetica* 44(1):39–45.
2005	Souza G.M., Pincus S.M., Monteiro J.A.F., The complexity-stability hypothesis in plant gas exchange under water deficit. *Brazilian Journal of Plant Physiology* 17(4):363–373.
in preparation	Monteiro J.A.F., Hiltbrunner E., Körner C., Biomass production of the tall tussock *Festuca orthophylla* in the Andean Altiplano.
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Posters and oral presentations

2008	Leaf dynamics of grazed tall tussock grass in the Bolivian Altiplano, XXIII Argentinian Congress of Ecology (RAE), San Luis, Argentina - oral presentation.
2005	Dynamical complexity of gas exchanges and higher network connectance improves homeostasis of plants under water deficit, XVII International Botanical Congress, Wien, Austria - oral presentation.
2002	Photosynthetic responses in function of different concentrations of CO_2 in two woody species from Cerrado in wet and dry season, 8^{th} Latin-American Congress of Botany, Cartagena de Indias, Colombia - poster.
2001	Climate and its influence in leaf gas exchange and water potential in Cerrado *sticto sensu* vegetation, 8^{th} Brazilian Congress of Plant Physiology, Ilhéus, Brazil - poster.

Scholarships

2004 (18 months)	Support for the Master in Switzerland - Federal Commission for Scholarships for Foreign Students (FCS).
2001 (12 months)	Scientific Iniciation of the São Paulo Research Foundation (FAPESP): 'Photosynthetic responses as a function of CO_2 concentration in two woody species of Cerrado vegetation during the wet and dry season'.

Computer skills

advanced	Macintosh and PC; R, Microsoft Office, GIMP, Inkskape, Photoshop, ImageJ.
basic	LaTeX, ArcGIS.

Languages

Portuguese and Spanish (mother languages), German and English.

Moderate skills in French.

Hobbies

Cycling, hiking, running, climbing, reading, photographing, cooking.